ASSEMBLY DYNAMICS FOR A CORAL-ASSOCIATED REEF COMMUNITY:

SPATIAL AND TEMPORAL PATTERNS, AND A TEST OF PRIORITY EFFECTS

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DEDICATION

This work is dedicated to the memory of Dr. Susan Williams for sharing her passion for marine ecology with myself and many others, encouraging women to pursue careers in science, and inspiring us to share science broadly with colleagues, politicians, and community members.

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ABSTRACT

A foundational goal of community ecology is to understand the drivers of variation in communities over spatial and temporal scales. This dissertation combines nondestructive, observational studies of natural variation within a coral-associated reef community over spatial and temporal scales, with a community manipulation that directly tested the effects of two common species on community assembly processes. The observational components of this research characterized the composition of coral-associated reef communities and investigated patterns in community composition relative to colony- and regional-scale environmental gradients. The results showed that colony-scale parameters influence the composition of these communities more than regional-scale parameters over both spatial and temporal scales. Colony size, depth, and percent live coral tissue were all correlated with changes in community composition in space and time. In addition to patterns associated with colony-scale parameters, communities varied along spatial gradients in wave height and chlorophyll-a. The composition of communities was more consistent in time than in space when comparing within-colony and between colony community dissimilarity metrics. Spatial surveys depicted non-random co-occurrence patterns between some of the commonly observed community members. By modeling probabilities of species arrival and departure relative to the presence of taxonomically similar species, temporal surveys of focal communities reinforced the importance of species interactions in structuring coral-associated reef communities and added a directional component to these potential species interactions. Community manipulations directly quantified the effects of two commonly observed protection mutualist species on the formation and maintenance components of community assembly. The results of these experiments indicated that these two species have inhibitory effects on the composition of the coral-associated community. These

effects were driven by species-specific responses to each of the mutualist species. This dissertation provides fundamental details about the natural variation in coral-associated communities, incorporates a community manipulation to directly test community assembly processes, and provides a template of analyses for characterizing spatial and temporal patterns in other communities.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Introduction

Community assembly

An ecological community is an assemblage of species that live within a shared environment and are connected through a network of potential and realized influences on each other. Understanding the community assembly dynamics (Diamond 1975) that drive the formation and maintenance of communities over various spatial and temporal scales is one of the fundamental goals of ecology. Which subset of species arrives to a community (i.e., community formation) hinges on successful dispersal or emigration (Fox et al. 2012; Basterretxea et al. 2013; Vaz et al. 2013) and favorable environmental characteristics (Belyea and Lancaster 1999; Thuiller et al. 2015). In addition, community formation is often affected by the order in which species arrive, through positive and negative, direct and indirect species interactions (Sutherland 1974; Connell and Slatyer 1977; Booth 1992). After species arrive to a community, the successful retention of species (i.e., community maintenance) depends on their fitness and survival in the community. These species-specific metrics are influenced by habitat quality (Hixon and Beets 1993; Macneil et al. 2009; Almeida et al. 2014) and species interactions (Connell 1961; Stallings 2008; Stier and Leray 2014). The structuring processes that operate on the formation and maintenance components of community assembly lead to observable patterns in the composition of communities, which can in turn be used to provide support for potential underlying processes (Schmitt and Holbrook 1999; Depczynski and Bellwood 2005; Paradise et al. 2008; Sim-Smith et al. 2013; Jankowski et al. 2015).

To investigate patterns in ecological communities and to illuminate relative support for potential mechanisms structuring communities, a combination of analyses can be used that consider variation in (1) single species occurrences, (2) community-level metrics (e.g., abundance of individuals, biomass, species richness, species evenness), and (3) multivariate community composition data. Analyses of individual species can depict important responses to environmental drivers, and some species can be utilized as indicator species for patterns in the broader community (King and Beazley 2005). Univariate community-level metrics of biomass

and species diversity can be very effective for identifying patterns in community composition, including shifts in species diversity over large spatial scales (Boltovskoy and Correa 2017), peaks in diversity relative to disturbances (Sousa 1979; Johst and Huth 2005; England et al. 2008), and associations between biomass and environmental drivers (Heenan et al. 2016). Species turnover, a quantification of the compositional difference between communities (Sørensen 1948), can provide valuable insight for understanding processes that lead to differences in community composition without leading to differences in the number of species (i.e., interchange of specific species between sites). Species turnover can be considered as a metric of diversity with which to compare the variability of communities between different groups of communities (Whittaker 1960; Martins et al. 2018). Species turnover can also be used to compare the composition of communities along a directional gradient relative to environmental characteristics (Silva et al. 2018), space, or time (Anderson et al. 2011). To directly investigate patterns in multivariate community composition data, ordination analyses can be utilized. These types of analyses include principal components analyses (PCA) and non-metric multi dimensional scaling (NMDS), both of which enable simultaneous consideration of numerous species observed across multiple communities. In addition, recent shifts to open-source statistical software packages have increased the use of hierarchical mixed models and non-linear models to evaluate complex patterns in communities over multiple scales (Bates et al. 2015; Gove et al. 2015; Pinheiro et al. 2016; R Development Core Team 2016).

Observational studies of naturally occurring communities are a core component of ecology. Surveys can often be conducted with minimal impact to the natural community. Basic patterns in compositional variation can be characterized. Patterns in variation can be considered over large spatial and temporal scales, and along broad gradients in environmental drivers (Freestone and Inouye 2015). However, inferences of underlying processes based on observed patterns should be approached with caution (Connor and Simberloff 1979; Wilson 1994; Fox 2013; Barner et al. 2018). The patterns expected for a given process may not be realized in communities that are exhibiting nonequilibrium dynamics (Loreau 2000; Hixon 2011). In addition, there is potential for complex interactions across multiple underlying processes in which the overall outcome does not reflect a linear combination of processes (Hixon and Carr 1997; Barner et al. 2018). Further, neutral theory and null models can explain some of the

patterns observed in communities (Connor and Simberloff 1979; Chave 2004; Hubbell 2005). These inherent complexities in the interpretation of community composition patterns should not deter observational studies. Instead, an awareness of these intricacies should encourage the cautious interpretation of observed patterns. Investigations into the mechanisms structuring communities can be strengthened through combinations of spatial and temporal surveys (Freestone and Inouye 2015). Moreover, observational studies can be paired with experiments that directly test for the effects of potential underlying mechanisms (Stier and Osenberg 2010; Miller and TerHorst 2012; Stier et al. 2013; Martins et al. 2018).

Study system

This research focuses on the semi-cryptic coral reef community associated with the scleractinian coral *Pocillopora meandrina* Dana, 1846. Pocilloporid corals provide an ideal habitat for studying community assembly dynamics because they: (1) form small, spatially discrete habitat patches, (2) are broadly distributed across much of the Indo-Pacific, and (3) host a diverse suite of fish and invertebrate species (Stella et al. 2010). In Hawai‘i, where this research takes place, *P. meandrina* is one of the most common corals, and in many areas, it provides the only branching reef structure.

The community associated with *Pocillopora* corals includes a collection of species that have been shown to have a mutualistic relationship with the host coral. Trapeziid crabs defend their *Pocillopora* host from the predatory crown-of-thorns sea star (Pratchett 2001; McKeon et al. 2012) and from the deleterious effects of vermetid epibionts (Stier et al. 2010). In addition to providing protective services to their host coral, trapeziid crabs can increase coral growth and survival by removing sediments from the coral tissue (Stewart et al. 2006). Similarly, snapping shrimp remove sediments from the coral tissue (Stier et al. 2012) and help protect their host coral against corallivores (Pratchett 2001; McKeon et al. 2012). Damselfishes sheltering within the branches of *Pocillopora* colonies can also promote growth and survival of the host coral through multiple mechanisms. The territorial behaviors of damselfish can minimize the predation of coral polyps by other reef fishes (Gochfeld 2009; Chase et al. 2014). Damselfish that exhibit a sleep-swimming behavior circulate the water between coral branches at night (Goldshmid et al. 2004). In addition, damselfishes that shelter within the coral’s branches provide the host coral with

excretion-based nutrient enrichment (Holbrook et al. 2008). These mutualistic species and many other species that associate with *Pocillopora* corals can be effectively surveyed with non-destructive survey techniques (Sin and Lee 2000).

Research goals

To study spatial scales of variation, sets of communities were surveyed at multiple sites spanning the entire coastline of the island of O‘ahu, Hawai‘i (Chapter Two). This combination of a high replication of surveys at small spatial scales and a large spatial distribution of survey sites enabled the use of hierarchical mixed models to compare variation in community composition with environmental gradients at both the colony- and site-scale. In addition to examining patterns in community level parameters, multivariate hierarchical mixed models were developed to depict species-specific patterns. Further, the co-occurrence of commonly observed species was analyzed to identify non-random patterns of habitat use relative to the distribution of other species.

To elucidate the consistency of these communities through time, focal communities were followed quasi-monthly for over three years (Chapter Three). Within-colony variation in community composition was analyzed relative to a temporal gradient and compared to between colony variation. The persistence of each species on individual host colonies was compared to their spatial occupancy across colonies. Mantel tests and linear regressions were used to investigate potential correlations between temporal variation in communities and synchronous fluctuations in regional environmental parameters. Transition probability models were developed to estimate the effect of functionally similar species on arrival and departure dynamics.

To directly test for ‘priority effects’, a potential mechanism of community assembly, colonies were arranged in an experimental grid and their associated communities were manipulated to create distinct community treatments (Chapter Four). The treatments focused on two commonly observed, protection mutualist species and followed a factorial design resulting in the following four treatment groups: (1) a pair of alpheid shrimps, (2) a pair of trapeziid crabs, (3) pairs of both alpheid shrimps and trapeziid crabs, or (4) an empty coral (control group). The experiment was divided into two sections to separately study how the presence of established protection mutualist species affected community formation and community maintenance. First,

the arrival of species to corals was recorded, and probabilities of species colonization were compared among treatments. Then, community composition was followed through time, and the trajectories of functional groups, as well as the trajectories of metrics characterizing community composition, were compared among treatments.

Overall, this dissertation characterizes the reef communities associated with *P. meandrina* in Hawai‘i. Patterns in the natural variation of these communities are explored over spatial and temporal scales. Probable associations between these patterns and environmental gradients at the colony- and site-scales are evaluated. Evidence for species-interactions as a potential mechanism structuring these communities is considered from species-specific patterns recorded through spatial and temporal surveys. To directly examine the role of species interactions, a community manipulation tests the effect of two species on community assembly processes. This dissertation's combination of observational and experimental research provides a template of analyses for investigating spatial and temporal patterns in ecological communities.

CHAPTER 2

Variation in coral-associated cryptofaunal communities across spatial scales and environmental gradients

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Abstract

Most of the diversity on coral reefs is in the cryptofauna, hidden organisms that inhabit the interstitial spaces of corals and other habitat-forming benthos. However, little is known about the patterns and drivers of diversity in cryptofauna. We investigated how the cryptofaunal community associated with the branching coral *Pocillopora meandrina* varies across spatial scales and environmental gradients. We performed non-destructive visual surveys of the cryptofaunal community on 751 *P. meandrina* colonies around the island of O‘ahu (30-73 colonies per site; 3-6 sites per region; 5 regions). We identified 91 species, including 48 fishes and 43 invertebrates. Most of these species were observed rarely, with only 19 species occurring on greater than 5% of surveyed colonies. Variation in community abundance and species richness was greatest at the scale of the coral colony and lowest at the site scale. Abundance and species richness increased with increasing colony size and maximum wave height, and decreased with increasing surface chlorophyll-a. In an analysis of species-specific responses, colony size, wave height, and chlorophyll-a were significant drivers of occurrence. Depth and percent live coral tissue were also identified as important correlates for community composition with distinct responses across taxa. Analyzing species-specific responses to environmental gradients documented a unique pattern for the guard crab *Trapezia intermedia*, which had a higher probability of occurring on smaller colonies (in contrast to 18 other common taxa). The results of a principal coordinates analysis on community composition and a co-occurrence analysis further supported *T. intermedia* as having a unique distribution across colonies, even in comparison to four other *Trapezia* species. Overall, these patterns emphasize the importance of host coral characteristics (i.e., colony size and percent live tissue) and physical characteristics of the

surrounding habitat (i.e., wave energy, chlorophyll-a, and depth) in structuring cryptofaunal communities, and characterize species-specific responses to environmental gradients.

Introduction

Most of the diversity on coral reefs is in the cryptofauna, the hidden species that inhabit the branches, crevices, and interstitial spaces of corals and other habitat-forming sessile organisms (Reaka-Kudla 1997; Plaisance et al. 2011). Reef-associated cryptofauna constitute 91% of the known species on coral reefs (Stella et al. 2010) and are a critical component of coral reef trophic webs. Cryptofauna capture and recycle nutrients by consuming very small prey items (e.g., plankton, detritus, coral mucus), and they are a primary food source for many reef fishes, including squirrelfishes, wrasses, triggerfishes, snappers, and groupers (Randall 1967; Enochs 2012; Leray et al. 2015). Despite their abundance and importance, reef cryptofauna are under-represented in traditional reef surveys and, as a result, relatively little is known about the composition of these communities and the ecological processes that structure them.

One of the most diverse coral-associated cryptofaunal communities is associated with living and dead corals in the family Pocilloporidae (Stella et al. 2010). Pocilloporids are structurally complex, reef-building corals that are common, especially on exposed reefs, and widespread throughout much of the Indo-Pacific. The relatively small size and spatial isolation of individual *Pocillopora* colonies facilitates studies of discrete, replicate communities. Given the tractable nature of these communities, *Pocillopora*-associated assemblages have been the focus of research on species interactions and cryptofaunal distribution since the 1960s. Previous research on *Pocillopora*-associated communities has identified cryptofauna-coral host mutualisms for trapeziid crabs, alpheid shrimps, and damselfishes. Crabs in the genus *Trapezia* and shrimps in the genus *Alpheus* help protect their host corals from corallivores, including the predatory gastropod *Drupella cornus* (McKeon and Moore 2014), the cushion star *Culcita novaeguineae* (McKeon et al. 2012; McKeon and Moore 2014), and the crown-of-thorns sea star *Acanthaster planci* (Pratchett 2001; McKeon et al. 2012: McKeon and Moore 2014; Rouzé et al. 2014). These mutualistic decapods also increase the growth and survival of host corals by removing sediments from the coral tissue (Stewart et al. 2006; Stier et al. 2012; Stewart et al. 2013; Rouzé et al. 2014) and reducing negative interactions with vermetid snails (Stier et al.

2010). Damselfishes associated with *Pocillopora* colonies promote coral growth and survival through a variety of mechanisms, including territorial defense that minimizes predation from other reef fishes (Gochfeld 2009; Chase et al. 2014), sleep-swimming behavior that circulates water between coral branches at night (Goldshmid et al. 2004), and excretion-based nutrient enrichment (Holbrook et al. 2008). In addition to describing coral mutualisms, several studies have reported that some species in the coral-associated community can affect the occurrence and survival of other species through predation and territorial behavior (Schmitt et al. 2009; Holbrook et al. 2011; Stier et al. 2013; Stier and Leray 2014; Leray et al. 2015).

Given the focus of *Pocillopora* research on species interactions and the considerable effort required to exhaustively sample cryptofaunal communities, most surveys of *Pocillopora*-associated communities can be fit into one of two categories: large visual surveys focused on a few key species (e.g., Sin and Lee 2000; Holbrook et al. 2008; Stier and Leray 2014), or thorough, albeit destructive, sampling limited to a small number of colonies (e.g., Austin et al. 1980; Coles 1980; Black and Prince 1983; Gotelli and Abele 1983; Britayev et al. 2017; López-Pérez et al. 2017). Previous surveys have identified host colony size as a strong correlate with the number of individuals and diversity of species in the associated community (Abele and Patton 1976; Stella et al. 2010; Holbrook et al. 2011). In addition, many studies have suggested that a decline in host coral health due to tissue bleaching or mortality shifts the composition of the decapod community from a few obligate species to a more diverse group of facultative species (Coles 1980; Stewart et al. 2006; Enochs and Hockensmith 2008; Plaisance et al. 2009; Stella et al. 2010; Stella et al. 2011; Enochs and Manzello 2012; Leray et al. 2012), although some obligate species, including *Trapezia* crabs, have been observed on dead coral colonies (Preston and Doherty 1990; Stella et al. 2011a; Head et al. 2015).

While some research has suggested that *Pocillopora*-associated communities vary over space as a result of environmental drivers (Abele 1976; Austin et al. 1980; Black and Prince 1983; López-Pérez et al. 2017), previous studies were limited in spatial extent (two to four sites) and did not directly investigate the correlation between specific environmental factors and community composition. Environmental factors including depth, reef zone, and wave energy can drive shifts in community composition for corals (Franklin et al. 2013; Gove et al. 2015), non-cryptic reef fishes (Nunes et al. 2013; Jankowski et al. 2015; Darling et al. 2017), and

cryptofaunal communities not directly associated with coral hosts (Klumpp et al. 1988; Depczynski and Bellwood 2005).

Here, we examined how environmental factors influence the composition of *Pocillopora*-associated cryptofaunal communities, providing a broader ecological context for the existing experimental work on these communities. We included measures of colony size and percent live tissue, factors highlighted in previous studies, to reflect the habitat quality of the host coral. We hypothesized that species exhibit taxon-specific responses across gradients of depth and wave energy, resulting in unique community compositions. We also considered the effect of host density, hypothesizing that the abundance of obligate species on each colony will decrease with increasing availability of adjacent host colonies. Further, we hypothesized that increasing benthic complexity at the site scale would decrease the species richness of the *Pocillopora*-associated community due to increased habitat structure available for facultative species. Finally, we investigated whether abundance or species richness increased with primary productivity (measured as satellite-derived surface chlorophyll-a). Whilst positive, negative, and unimodal patterns have been observed between productivity and species richness (Mittelbach et al. 2001), here we expected community abundance and species richness to increase with chlorophyll-a because some of the species feed directly on plankton and because our study sites are oligotrophic, i.e., where the positive part of a unimodal relationship between productivity and species richness would occur.

To analyze patterns over these environmental gradients, we non-destructively surveyed the communities associated with 751 *Pocillopora meandrina* colonies across 19 sites from 5 regions around the island of O‘ahu, Hawai‘i. We characterized the fish and invertebrate species found on *P. meandrina*, partitioned variation in the community across spatial scales, and quantified correlations between both community abundance and species richness, and possible environmental drivers. Further, we investigated patterns in community composition by identifying species-specific responses to environmental factors and non-random species co-occurrences.

Methods

Surveys

To characterize the *P. meandrina*-associated community, we surveyed 751 colonies across 19 sites around the island of Oʻahu (Fig. 2.1) from September 2013 to March 2015. Sites were stratified into five regions (east, south, west, north, and Kāneʻohe Bay), each characterized by different wave regimes, which is an important variable structuring coral communities (Dollar 1982; Franklin et al. 2013; Gove et al. 2015). Prior modeling studies were used to identify potential sites within areas that were predicted to have high *P. meandrina* cover (Franklin et al. 2013), and adequate *P. meandrina* density was verified *in situ* before each survey.

Surveys were conducted on SCUBA with one diver consistently surveying the cryptic communities and other diver(s) collecting colony-scale environmental characteristics. Focal colonies were selected haphazardly along a compass heading at least two meters from the previous colony and matching a randomly generated size class. To survey the *Pocillopora*-associated communities, a flashlight and side-to-side search pattern were used, and species identities and abundances were recorded for all associated fauna species. Visual surveys provide a conservative estimate of community abundance and species richness particularly for organisms that are either very small (<3 mm), transparent (e.g., *H. depressa*), or associated with habitat at the base of the colony (e.g., *Trapezia* spp. juveniles, see Preston 1971). We did not observe trapeziid crabs until they approached 5 mm, a size at which they spend more time out on the colony's branches (Preston 1971) and were consistently identifiable to the species level. For a few other taxa, we could not consistently see distinguishing features and, therefore, we grouped these species to higher taxonomic levels: hermit crabs, *Drupella* snails, vermetid snails, and *Spirobranchus* worms. In addition, "*Sebastapistes* spp." was used for a set of three visually similar scorpionfish species (*S. fowleri*, *S. galactacma*, and *S. ballieui*). Despite these limitations, a previous study that used a similar technique confirmed that visual surveys were 97% accurate in identifying species and estimating abundance of the cryptofaunal community (Sin and Lee 2000).

For each focal *P. meandrina*, divers recorded the colony size, maximum inter-branch distance, percent live coral tissue, and depth (Table 2.1). In addition, a photograph was taken of

each colony from about 1-2 m above the substratum. These photographs were used to estimate the density of *Pocillopora* spp. colonies in the area immediately surrounding each focal colony (Table 2.1). Using geospatial software ArcGIS 10.3 (ESRI 2014), maximum significant wave height, bathymetric rugosity (Franklin et al. 2013), and mean surface chlorophyll-a (NASA 2018) were estimated at the site scale (Table 2.1).

Statistical Analysis

Community Characterization: To estimate whether or not the full community was surveyed, a species accumulation curve with a Chao estimate of asymptotic species richness was created (function "specpool" in *R* package *vegan*; Oksanen et al. 2017). A species rank abundance curve was plotted to visualize the balance of common to rare species and to identify reasonable cutoffs for commonly occurring species to be used in community composition analyses.

Community Metrics: Community abundance (i.e., total number of individual organisms on the host colony) and species richness values were calculated for each colony focusing on the subset of species that were observed on at least 1% of colonies (i.e., ≥8 of 751 colonies). To determine relative levels of variation in abundance and species richness over spatial scales, we ran a Poisson generalized linear mixed model (GLMM, function "glmer" in *R* package *lme4*; Bates et al. 2015) for each community metric, with site and region as nested random effects to account for the spatial structure of the data and an observation-scale random effect to account for over dispersion (Model 2.S1). The conditional R^2, an estimate of variance explained by all factors included in a mixed model (function "r.squaredGLMM" in *R* package *MuMIn*; Bartoń 2016), was used to estimate how much total variation in abundance and species richness was explained. Random effect variance estimates were used to determine the relative amount of variation explained at each spatial scale.

We ran additional Poisson GLMMs for community abundance and species richness with colony and site scale environmental factors (Table 2.1) as fixed effects, site and region as nested random effects, and an observation-scale random effect to account for over dispersion (Model 2.S2). Environmental characteristics measured at the colony and site scales (Table 2.1) were centered and scaled, and correlation coefficients were evaluated with a threshold of ±0.7 prior to

inclusion in models (Table 2.S1). To quantify the relative importance of each environmental factor, all possible models (n=256) were run (function "dredge" in *R* package *MuMIn*; Bartoń 2016); for the subset of models that contained each variable, the associated model probabilities were summed (Anderson 2008). In addition, a weighted multi-model average was calculated, using models with a ΔAIC <4, to estimate the effect size of each predictor. These analyses were repeated for the subset of species that were observed on 5% or more of colonies; the results were qualitatively similar and are not presented.

Species-Specific Patterns: To examine shifts in community composition, we focused on the subset of species that occurred on 5% or more of surveyed colonies (i.e., ≥38 of 751 colonies). To evaluate patterns in species occurrence over spatial scales and environmental drivers, we ran a set of binomial GLMMs that had probability of occurrence as the response variable and random effects to account for species identity and survey structure (colony nested in site nested in region) as the base model (Table 2.S2). Three additional model components were compared in the set of GLMMs (Table 2.S2): (1) species-specific patterns over sites and regions, (2) effects of environmental factors averaged across all species, and (3) species-specific responses to the environmental factors (Model 2.S3). To estimate the variation in occurrence explained by each model component, marginal and conditional R^2 values were calculated for each model (function "r.squaredGLMM" in *R* package *MuMIn*; Bartoń 2016).

An initial set of GLMMs was run that included all the environmental factors in Table 2.1. Three of these environmental factors (inter-branch distance, density of *Pocillopora* colonies, and rugosity) had non-significant effects and showed minimal variation in species-specific responses. These factors were dropped and a simpler model with five environmental factors (colony size, percent live coral tissue, depth, wave energy, and chlorophyll-a) was used. Residual plots of all models were visually inspected and no strong deviations from homoscedasticity or normality were observed.

Species Co-occurrence: To visualize patterns of species co-occurrence, we ran a principal coordinates analysis on colony scale community composition for the species observed on 5% or more of colonies. In addition, patterns of species co-occurrence were directly compared (function "cooccur" in *R* package *cooccur*; Griffith et al. 2016) by classifying species pairs as having positive (i.e., co-occur more often than expected by chance alone), negative (i.e., co-

occur less often than expected by chance alone), or random associations (i.e., co-occurrence is not different than expected by chance alone) based on the probabilistic model of species co-occurrence from Veech (2013).

Results

Community Characterization: For the 751 *P. meandrina* colonies surveyed across 19 sites, the average colony size was 21.1±9.2 cm (mean±SD, Table 2.1). An average of 4 species and a maximum of 13 species per colony were observed. In total, 5,887 individuals of 91 different species (48 fishes and 43 invertebrates, Table 2.S3) were observed in association with *P. meandrina* colonies (n=751). A rarefaction plot indicated that additional surveys would identify more species with an estimated 115.2±13.7 total species (mean±SE; Chao estimate) associated with *P. meandrina* (Fig. 2.2a). Decapods comprised 51% of all individuals and 25% of all species observed. Most species were observed at low colony-scale abundances (1-3 individuals per species per colony); two species were observed at high colony-scale abundances, the gall-forming coral crab *Utinomiella dimorpha* (mean = 7.9 individuals per colony) and the damselfish *Dascyllus albisella* (mean = 5.3 individuals per colony, Fig. 2.2b).

Of the 91 species found, only one third (10 fishes and 21 invertebrates) were observed on more than 1% of colonies (Table 2.2, Fig. 2.2c), and the 19 species that were observed on ≥5% of surveyed colonies (Table 2.2) accounted for 90% of all observations (4,531 of 5,037 specimens, Fig. 2.2c). The 19 most common species included nine known coral mutualists: five species of *Trapezia* crabs, one species of *Alpheus* shrimp, one species of *Harpiliopsis* shrimp and two species of pomacentrid fishes (Table 2.2).

Community Metrics: Based on a GLMM with only random effects (Model 2.S1), variation in cryptofaunal species richness was 10.6% at the region scale, 5.2% at the site scale, and 84.2% at the colony scale (Fig. 2.S1a). The west and north regions were estimated to have an average of ~5 species per colony, the south and east regions were estimated to have an average of ~3.5 species per colony, and the Kāneʻohe region was estimated to have an average of ~2.7 species per colony (Fig. 2.S2a). Variation in community abundance was also predominately at the colony scale (95.1%), with 2.8% at the region scale and 2.1% at the site scale (Fig. 2.S1b).

The differences in abundance between regions followed a similar pattern as described for species richness (Fig. 2.S2b).

In the GLMM for species richness with spatial random effects and environmental factors as fixed effects (Model 2.S2), 42.8% of variation in species richness was explained by environmental factors (Table 2.1), 0.2% was accounted for at the region scale, 7.3% at the site scale, and 49.6% at the colony scale (Fig. 2.S1a). For community abundance, 48.8% of variation was explained by environmental factors (Table 2.1), <0.1 % was accounted for at the region scale, 2.3% at the site scale, and 48.8% at the colony scale (Fig. 2.S1b). Three environmental factors (colony size, wave energy, and chlorophyll-a) had strong model support (>85 %) and average effect sizes that were significantly different from zero (Fig. 2.3) for both abundance and species richness. For the abundance model, percent live coral tissue and inter-branch distance had average effect sizes that were small but significantly different from zero (Fig. 2.3). Abundance increased by <2 individuals per colony with an increase in percent live tissue from 0 to 100% (Fig. 2.S3m), and decreased by <3 individuals per colony with increasing inter-branch distance from 1.5 to 45 mm (Fig. 2.S3o). Across the range of colony sizes surveyed (4 to 78 cm diameter, Table 2.1), the model predicted an increase from 0 to 45 species and from 0 to 400 individuals per colony with increasing colony size (Fig. 2.S3a & 2.S3i). With increasing maximum wave energy over the range surveyed (Table 2.1), the model predicted an increase from 2 to 5 species and from 3 to 12 individuals per colony (Fig. 2.S3b & 2.S3j). The model predicted a decrease from 4 to 2.5 species and from 3 to 6 individuals per colony with increasing surface chlorophyll-a levels (Fig. 2.S3c & 2.S3k) over the range surveyed (Table 2.1). For all other environmental factors included (i.e., depth, percent live coral tissue, density of *Pocillopora*, inter-branch distance, and rugosity), species richness was predicted to change by <1 species per colony and community abundance was predicted to change by 3 or less individuals per colony (Fig. 2.S3d to 2.S3h & Fig. 2.S3l to 2.S3p) over the ranges surveyed (Table 2.1).

Species-Specific Variation: Of the 91 species observed, five species were observed at all sites (*Alpheus lottini*, *Ophiocoma pica*, *Harpiliopsis depressa*, *Trapezia intermedia*, *T. tigrina*), and 31 species were observed at only one site (Table 2.S3). Relative to other survey sites, Kāneʻohe Bay sites had high proportions of damselfishes (i.e., *Plectroglyphididon johnstonianus*, *D. albisella*) and low proportions of predatory fishes (e.g., *Paracirrhites arcatus*, *Caracanthus*

typicus) (Fig. 2.4). Three of the five species of *Trapezia* crabs (i.e., *T. digitalis*, *T. bidentata*, *T. flavopunctata*) had occurrence rates approaching zero at all three Kāne‘ohe Bay sites, Lanikai, Waikiki, Ewa Beach, and Yokohama (Fig. 2.4; site names in Table 2.S4). The relatively unique community composition for colonies from sites in Kāne‘ohe Bay was documented by a canonical analysis of principal coordinates constrained by survey site (Fig. 2.S4).

Comparisons across binomial GLMMs run with different model components showed that species-specific patterns explained most of the variation in occurrences (Table 2.2, Fig. 2.S5a & 2.S5b). The base model including random effects for species identity and the hierarchical structure of the surveys explained 30.4% of the variation in species occurrences (Table 2.S2: Base Model). Most of this variation, 21.2%, was due to species identity, i.e., some species were more common than others overall. The remaining variation, 9.2%, was allocated to spatial scales reflecting that some locations (i.e., colonies, sites, or regions) had higher probabilities of occurrence for all species. Including species-specific patterns at the site and region scales nearly doubled the explained variation to 57.1% (Table 2.S2: Compositional Variation over Spatial Scales). Most of this variation was at the colony scale, followed by site scale, and then region scale (Fig. 2.S5a).

The full GLMM, which included average environmental effects, species-specific variation over spatial scales, and species-specific variation over environmental factors, explained 68.2% of the variance in occurrences (Table 2.S2: Full Model). This was 8% more variation than any other model, supporting the complementary explanatory power of species-specific patterns over environmental gradients and species-specific patterns over spatial scales. The average response to environmental factors across all species explained 13.2% of variance in occurrences (Table 2.S2). Three environmental factors had effect sizes that were significantly different from zero: colony size (0.99±0.12 SE, Fig. 2.5a), wave height (0.79±0.24 SE, Fig. 2.5b), and chlorophyll-a (-0.71±0.30 SE, Fig. 2.5c). Including species-specific responses for each of five environmental factors significantly improved the model fit (Chi-squared likelihood ratio tests, function “anova” in *R* base *stats* package) supporting significant variation in community composition across these environmental gradients. The standard deviation for species-specific responses to environmental factors was greatest for chlorophyll-a (0.99), followed by depth (0.85), wave height (0.64), colony size (0.48), and percent live coral tissue (0.37) (Fig. 2.5f).

Species-specific responses to depth and percent live coral tissue depicted distinct shifts in the community over these gradients with some species having higher probability of occurrence at low values and other species having higher probability of occurrence at high values (Fig. 2.5d and 2.5e). For example, guard crab *T. digitalis*, coral gall crab *U. dimorpha*, flattened coral shrimp *H. depressa*, and coral croucher *C. typicus* had higher probabilities of occurrence on shallower corals; while guard crab *T. tigrina*, brittlestar *O. pica*, damselfish *D. albisella*, and hawkfish *P. arcatus* had higher probabilities of occurrence on deeper corals; and guard crab *T. intermedia* and snapping shrimp *A. lottini* had no change in probability of occurrence over the depth range surveyed (Fig. 2.5e).

Species Co-occurrence: The guard crab, *T. intermedia*, had the highest probability of occurrence and showed a distinct negative response to colony size (Fig. 2.5a). *T. intermedia* was also separated from the other species (including four other *Trapeziid* crab species) in a principal coordinates analysis of the community (Fig. 2.6a). A co-occurrence analysis of 171 pairs of the commonly observed species found that 55.6% were non-random: 65 species pairs occurred more frequently than expected (i.e., positive co-occurrences), and 30 species pairs occurred less frequently than expected (i.e., negative co-occurrences). *T. intermedia* was in 26.7% of all negative co-occurrences (Fig. 2.6b), including negative co-occurrences with three of the other *Trapezia* species (*T. flavopunctata*, *T. tigrina*, and *T. bidentata*). Of the remaining *Trapezia* pairs, only one other was a negative co-occurrence (*T. tigrina – T. digitalis*), three were positive (*T. digitalis – T. flavopunctata*, *T. flavopunctata – T. bidentata*, and *T. digitalis – T. bidentata*), and three were random (*T. intermedia – T. digitalis*, *T. flavopunctata – T. tigrina* and *T. tigrina – T. bidentata*).

Discussion

Our results documented spatial scales of variation in cryptofaunal communities associated with *P. meandrina* colonies and the importance of environmental factors in structuring community composition. Patterns in community abundance and species richness were similar with the largest amount of spatial variation observed at the colony scale (Fig. 2.S1) and strong correlations for both community metrics with colony size, maximum wave height, and surface chlorophyll-a (Fig. 2.3). Species-specific responses to environmental factors revealed

additional shifts in the community across a depth gradient and a range of percent live coral tissue, and presented a unique occurrence pattern for the most commonly observed trapeziid crab.

High variation in the cryptofaunal community at the colony scale indicates the importance of colony quality factors in structuring the associated community. Colony size, one metric of colony quality, had the largest correlation with abundance and species richness (Fig. 2.3), with shifts in predicted values an order of magnitude larger than across the range of any other factor (Fig. 2.S3). The increase in species richness with increasing colony size is consistent with species-area relationships (Arrhenius 1921) and previous studies of *Pocillopora*-associated communities (Stella et al. 2010; Holbrook et al. 2011; Head et al. 2015; Britayev et al. 2017). Our results suggest that there are additional, unmeasured colony quality factors because colony scale variation remained relatively high in the model that included colony size, percent live coral tissue, and inter-branch distance (Fig. 2.S1). Colony quality factors to which species may be responding could include colony age, symbiont clade, or complexity of interstitial microhabitats.

At the regional scale, cryptofaunal communities had higher abundance and species richness along the northern and western shorelines, average values along the southern and eastern shorelines, and relatively low values within Kāne‘ohe Bay (Fig. 2.S2). Environmental factors including wave height and surface chlorophyll explained most of this regional-scale variation (Fig. 2.S1). Community abundance and species richness increased with increasing wave height (Fig. 2.S3b & 2.S3j). This trend aligns with observed regional weather patterns, such as strong winter storms create exceptionally large waves along the NW coasts, the SE coasts have a more consistent level of wave energy with occasional storm driven peaks that are generally smaller than the NW storms, and Kāne‘ohe Bay is the most sheltered region surveyed (Fletcher et al. 2008). Previous work has quantified the importance of wave energy and water movement for structuring benthic cover (Franklin et al. 2013; Gove et al. 2015), and the community composition of both non-cryptic and cryptic reef fishes (Nunes et al. 2013; Depczynski and Bellwood 2005). Maximum wave height can be a metric of disturbance for coral reef communities. The increase in species richness observed in this study from colonies at sheltered sites to colonies at sites with large seasonal waves corresponds with the expected shift

in diversity among habitats with small disturbances to habitats with an intermediate level of disturbances (Connell 1978).

Cryptofaunal community abundance and species richness decreased with increasing surface chlorophyll-a, a measure of productivity (Fig. 2.S3c & 2.S3k). Previous work has found that there is often a correlation between diversity and productivity, but the direction of this relationship shows high variation over different communities and spatial scales (Cornell and Karlson 2000; Mittelbach et al. 2001; Chase and Leibold 2002). For this study, surface chlorophyll-a was estimated from satellite data at the site scale. At this resolution, chlorophyll-a had approximately the same value for all three sites in Kāneʻohe Bay, 4.13 mg m^{-3}, almost double the next highest chlorophyll-a estimate (Table 2.1). Thus, in the context of this study, chlorophyll-a may represent the distinctiveness of Kāneʻohe Bay, an estuary which receives high freshwater and sediment input from various streams and frequent orographic rainfall on the adjacent mountain range (Jokiel 2004), rather than variability in productivity across all sites. The relatively low abundance and species richness observed in Kāneʻohe Bay may reflect that habitat characteristics within the bay are not preferred habitat for some species, that restricted exchange into Kāneʻohe Bay may limit dispersal and prevent less common species from becoming established, or a combination of both.

Percent live coral tissue, depth, inter-branch distance, density of *Pocillopora* colonies, and rugosity did not have a significant effect on cryptofaunal species richness (Fig. 2.3). While previous work has demonstrated species-specific preferences based on inter-branch distances, e.g., *P. arcatus* prefers larger distances (Kane et al. 2009), our study did not support a correlation between species richness and inter-branch distance or species-specific patterns across colonies with differing inter-branch distances. We did observe higher abundances on colonies with smaller inter-branch distances (Fig. 2.3). This pattern has also been recorded for communities associated with acroporid corals, with greater abundances of cryptofauna found on tightly branched *Acropora* spp. than on arborescent *Acropora* spp. (Vytopil and Willis 2001). Habitat complexity is known to be positively correlated with abundance and diversity of non-cryptic reef-associated fishes (Gratwicke and Speight 2005; Darling et al. 2017), yet our results showed that these factors (i.e., density of *Pocillopora* colonies and rugosity) were not significantly correlated with species richness nor were there substantial species-specific patterns relative to

these factors. These results suggest either that these factors do not matter or that the scales at which these factors were measured (Table 2.1) were not appropriate for the *P. meandrina*-associated community. Species richness was not related to depth or percent live coral tissue, although species-specific trends were observed across these two factors, suggesting that species may filter in and out over these environmental gradients, thereby concealing a significant pattern when considering species richness. This outcome elucidates the benefit of considering species-specific responses to identify shifts in communities over environmental gradients that are not associated with significant changes in community-scale metrics.

Similar to variation in community metrics, most species-specific variation in community composition was at the colony scale (Fig. 2.S5). Environmental factors and species-specific responses to these factors accounted for some of the variation in species-specific occurrences at the colony and region scales, yet site scale variation remained relatively high (Fig. 2.S5b) suggesting that species responded to unmeasured factors at the site scale. Variation at the site scale could be due to constraints in local dispersal or habitat quality of the area surrounding the host corals, e.g., coral cover or adjacent habitat complexity (with a finer resolution than was considered here). The full model accounted for 68% of the variation in species-specific probability of occurrence, with the remaining 32% of variation in occurrence due to species-specific patterns at the colony scale (Model 2.S3). Species-specific patterns at the colony scale that were not explained by the environmental factors or associated with colony identity are likely the result of species-specific responses to unmeasured colony scale metrics of habitat quality. This could include order-of-arrival community assembly dynamics, such as priority effects (Shulman et al. 1983; Almany 2003) with species avoiding or preferring colonies based on community composition, or the complexity of inter-branch microhabitats.

The environmental drivers emphasized as strong correlates for species richness, i.e., colony size, wave height, and surface chlorophyll-a, had limited variation in species-specific responses. Almost all commonly observed species (with the exception of guard crab *T. intermedia*) had a higher probability of being observed on larger colonies than smaller ones (Fig. 2.5a). Most of the variation in species-specific responses to colony size was due to differences in the smallest size on which each species had a high probability of occurrence. For example, the hawkfish *P. arcatus*, damselfish *P. johnstonianus*, and guard crab *T. flavopunctata* were

observed with low probability until the colony was relatively large (Fig. 2.5a). Species-specific responses to wave height were fairly consistent, with the average trend of increased probability of occurrence with increasing wave height. Two exceptions, the damselfish *D. albisella* and the guard crab *T. intermedia*, had a modest decrease in their probability of occurrence with increasing wave height (Fig. 2.5b). For most species, the probability of occurrence decreased with increasing surface chlorophyll-a, although the opposite trend was observed for a few species, including the damselfish *D. albisella* and the wrasse *T. duperrey* (Fig. 2.5c).

There was no change in overall probability of occurrence with varying percent live coral tissue yet distinct species-specific patterns were observed (Fig. 2.5d). Some known coral-obligate species, including guard crab *T. intermedia*, snapping shrimp *A. lottini*, and flattened coral shrimp *H. depressa*, had higher probabilities of occurrence with higher percent live host coral tissue (Fig. 2.5d). In contrast, two species of brittle stars (*Ophiocoma pica* and *O. erinaceus*) were observed more often on colonies with lower proportions of live tissue (Fig. 2.5d). Previous studies have found different responses to the percent of live coral across different functional groups. For example, a higher proportion of live coral is associated with a higher diversity of reef fishes (Rasher et al. 2013) and a lower diversity of cryptic motile invertebrates (Coles 1980; Enochs and Hockensmith 2008; Enochs and Manzello 2012; Leray et al. 2012). Prior studies have shown that the invertebrate communities associated with dead corals are mainly, although not exclusively (Head et al. 2015), composed of facultative species with higher diversity per colony and higher variability across corals (Coles 1980). Our study confirms a shift from obligate to facultative species as the percent of live coral tissue declines, including a small increase in community abundance but no overall change in species richness.

Although depth had no overall effect on the probability of occurrence, there were strong species-specific responses from species across the depth gradient (Fig. 2.5e). These species-specific patterns are likely due to variation in recruitment and survival rates for each species across the depth gradient, which have been shown to structure the depth range of a *Pocillopora*-associated goby, *Paragobiodon xanthosoma* (Smallhorn-West et al. 2017). Shifts in species composition over depth gradients have been previously shown for both cryptic reef fish communities (Depczynski and Bellwood 2005) and non-cryptic reef fishes assemblages (Nunes et al. 2013; Jankowski et al. 2015; Darling et al. 2017).

In addition to revealing shifts in community composition across environmental factors, our species-specific GLMM depicted an intriguingly unique response to coral colony size for the most commonly observed species, *T. intermedia*. Unlike all other common species, the probability of occurrence of *T. intermedia* was higher for smaller colonies than for larger colonies (Fig. 2.5a) despite being observed across a broad range of colony sizes (7 to 65 cm). Of the five trapeziid species observed, *T. intermedia* was of a similar body size to all other species except *T. flavopunctata* which was distinctively larger than the other species, suggesting that the unique relationship between *T. intermedia* occurrence and colony size was not driven by body size differences. For the other environmental factors, the probability of *T. intermedia* occurrence was either largely unaffected (i.e., wave height, surface chlorophyll-a, and depth) or followed a similar pattern to other obligate species (i.e., percent live coral tissue). The observation that *T. intermedia* had a high probability of occurring on smaller colonies suggests that *T. intermedia* is one of the first species to colonize *P. meandrina*. Previous studies focused on the decapod communities associated with *P. meandrina* also noted that *T. intermedia* was the predominate trapeziid on small colonies (Barry 1965; Preston 1971; Huber and Coles 1986). A PCoA further supported unique characteristics of the distribution of *T. intermedia*, which was separated from other species in multidimensional space (Fig. 2.6a). A co-occurrence analysis found that *T. intermedia* occurred less often than expected by chance with three of the four other *Trapezia* crab species (Fig. 2.6b) likely due to competitive behavior. The patterns we observed for *T. intermedia* are consistent with the patterns expected for a species that is a good colonizer (first to arrive to small colonies) but a poor competitor (not often observed with congeneric species).

While our analyses focused on the most common species, our surveys also provided information regarding the rare cryptofaunal species inhabiting *P. meandrina*. Our results were consistent with the hypothesis that most of the species richness in reef cryptofauna is due to rare species (Austin et al. 1980; Plaisance et al. 2009; Stella et al. 2010; Plaisance et al. 2011), with 60 of 91 species observed on <1% of colonies, and 22 species observed on only one colony (Fig. 2.2c). Interestingly, some of the species that were rare in our surveys of *P. meandrina* colonies are relatively common in the larger reef ecosystem (e.g., the surgeonfish *Acanthurus triostegus* and the urchin *Echinothrix diadema*), suggesting that these species are transient in the context of

P. meandrina communities, temporarily associated with the colony despite it not being their primary habitat (Sgarbi and Melo 2017).

Previous work has highlighted the importance of certain *Pocillopora*-associated species and their species interactions for the host coral's health and survival as well as the structure of the cryptic community. This study provides context for this existing body of literature by characterizing naturally occurring patterns in the community relative to environmental factors and partitioning variation in the community across spatial scales. While some trends in community composition emerged at site and regional scales, the highest level of variation was at the colony scale. Our results emphasize the importance of colony size, wave height, and surface chlorophyll-a for driving the composition of cryptofaunal communities associated with *P. meandrina*. In addition, our study documented a shift in community composition over both depth and percent live coral tissue largely driven by species-specific patterns. Unique species-specific patterns for *T. intermedia* were identified, and we recommend further examination of the role of this species in community assembly processes. This study strengthens our understanding of how cryptofaunal reef communities, where most of the diversity on coral reefs is hidden, vary across environmental gradients.

Table 2.1. Environmental driver variables, including the source of data, description of variable, unit, mean value, and range of values. Means and ranges are calculated for all 751 *Pocillopora* colonies surveyed, except for inter-branch distance, which was measured for only 716 colonies, and density of *Pocillopora*, which was available for 743 colonies.

Variable	Source	Description	Units	Mean	Range
Colony Size	measured *in situ* to the nearest cm	habitat size; colony volume transformed to a linear estimate $(H \times D_1 \times D_2)^{1/3}$ where H is colony height, D_1 is longest diameter, and D_2 is longest orthogonal diameter	cm	21	4-78
Percent Live Coral Tissue	visually estimated *in situ* to the nearest 5%	habitat quality; percent of the *Pocillopora* colony that is covered in live coral tissue	%	86	0-100
Inter-Branch Distance	measured *in situ* to the nearest mm	interstitial space of the colony; maximum of five values for the distal distance between two adjacent branches with branch pairs haphazardly selected such that one pair was near the top center and the other four pairs were on the sides of the colony	mm	18.7	1.5-45
Depth	measured *in situ* with 0.3 m precision	depth at the base of the focal colony	m	9.5	0.6-31.1
Density of *Pocillopora*	derived from a top down photograph centered on the focal colony	count of *Pocillopora* colonies in the adjacent habitat divided by area of substrate in photograph of habitat	*Pocillopora* m^{-2}	1.0	0.1-7.4
Wave Height*	SWAN hindcast model (v40.51, 2006) forced with 2000-2009 spectral wave data from WAVEWATCH III (v3.14, Tolman 2009)	mean model predicted maximum significant wave height validated with comparisons to *in situ* data from NOAA wave buoys (Franklin et al. 2013)	m	2.6	0.8-5.2
Rugosity*	derived from a synthesis of LIDAR and SONAR data (Hawaii Mapping Research Group 2011)	GIS modeled ratio between the surface area and the planimetric area of a depth grid for central grid cells and their 8 surrounding neighbor cells (Franklin et al. 2013)	ratio	1.003	1.000-1.013
Chlorophyll-a*	Moderate Resolution Imaging Spectroradiometer (MODIS) 2008-2015 data from the Aqua satellite (NASA 2018)	mean near-surface chlorophyll-a concentration for January from measurements of color band ratios (spanning the 440-570 nm spectral regime) based on remotely sensed reflectance data	mg m^{-3}	1.34	0.07-4.13

*These factors are estimated at the site scale.

Table 2.2. Family, genus, species, species codes, % of regions, % of sites, % of colonies, average number of individuals observed on a colony, depth range, and % live coral tissue range for fish (n=10) and invertebrate (n=21) species observed on ≥1% of surveyed *Pocillopora meandrina* (n=751 colonies). Species are listed in descending order of % of colonies inhabited, with species observed on ≥5% of colonies listed in bold. Known coral mutualist species are noted with an *.

Family	Genus	Species	Spp. Code	% of Regions	% of Sites	% of Colonies	Avg. per colony	Depth (m)	% Live Coral Tissue
***Trapeziidae**	***Trapezia***	***intermedia***	**TRIN**	**100**	**100**	**59.0**	**1.6**	**0.6 - 31.1**	**20 - 100**
Ophiocomidae	***Ophiocoma***	***pica***	**OPPI**	**100**	**100**	**45.0**	**1.6**	**1.5 –30.5**	**0 - 100**
***Palaemonidae**	***Harpiliopsis***	***depressa***	**HADE**	**100**	**100**	**34.1**	**1.7**	**0.9 – 24.7**	**0 - 100**
***Alpheidae**	***Alpheus***	***lottini***	**ALLO**	**100**	**100**	**33.7**	**1.4**	**0.6 – 26.8**	**30 – 100**
***Trapeziidae**	***Trapezia***	***tigrina***	**TRTI**	**100**	**100**	**27.7**	**1.8**	**1.5 – 26.2**	**30 - 100**
Scorpaenidae	***Sebastapistes***	**spp.**	**SESP**	**100**	**89**	**23.0**	**1.9**	**2.4 – 30.5**	**30 - 100**
Cirrhitidae	***Paracirrhites***	***arcatus***	**PAAR**	**80**	**79**	**23.0**	**1.3**	**3.4 – 31.1**	**0 - 100**
***Trapeziidae**	***Trapezia***	***digitalis***	**TRDI**	**100**	**79**	**16.5**	**1.5**	**2.1 – 19.5**	**45 – 100**
Cryptochiridae	***Utinomiella***	***dimorpha***	**UTDI**	**80**	**42**	**16.5**	**7.9**	**3.0 - 18.3**	**30 - 100**
Scorpaenidae	***Sebastapistes***	***coniorta***	**SECO**	**100**	**89**	**15**	**1.9**	**2.1 – 19.5**	**30 - 100**
Caracanthidae	***Caracanthus***	***typicus***	**CATY**	**80**	**79**	**9.9**	**1.5**	**2.4 – 16.8**	**50 - 100**
***Pomacentridae**	***Plectroglyphididon***	***johnstonianus***	**PLJO**	**100**	**74**	**9.2**	**1.3**	**2.1 – 26.2**	**0 - 100**
***Pomacentridae**	***Dascyllus***	***albisella***	**DAAL**	**100**	**58**	**9.2**	**5.3**	**1.5 – 30.2**	**0 - 100**
***Trapeziidae**	***Trapezia***	***bidentata***	**TRBI**	**100**	**58**	**7.5**	**1.6**	**2.1 – 18.0**	**45 – 100**
Labridae	***Thalassoma***	***duperrey***	**THDU**	**100**	**53**	**6.9**	**1.4**	**2.1 – 20.1**	**5 - 100**
Ophiocomidae	***Ophiocoma***	***erinaceus***	**OPER**	**100**	**79**	**6.4**	**1.3**	**2.7 – 20.4**	**0 - 100**
***Trapeziidae**	***Trapezia***	***flavopunctata***	**TRFL**	**100**	**68**	**6.1**	**1.7**	**2.1 – 16.8**	**50 - 100**
Sabellidae	***Sabellastarte***	***spectabilis***	**SASP**	**60**	**32**	**5.7**	**2.5**	**2.1 – 18.3**	**0 – 100**
Paguroidea	**unidentified**		**DIOG**	**60**	**53**	**5.3**	**2.4**	**2.4 – 19.8**	**0 - 100**
Cirrhitidae	*Amblycirrhitus*	*bimacula*	AMBI	100	42	4.3	1.2	3.0 - 14.3	0 - 100
Echinometridae	*Echinometra*	*mathaei*	ECMA	80	53	3.6	1.5	4.3 – 29.6	0 - 100
Muricidae	*Quoyula*	*monodonta*	QUMO	80	42	2.8	1.6	2.7 – 17.7	50 - 100
Domeciidae	*Domecia*	*hispida*	DOHI	80	47	2.4	1.4	3.4 – 19.8	40 – 100
Xanthidae	*Pseudoliomera*	*speciosa*	PSSP	100	68	2.3	1.4	2.1 – 14.3	75 - 100
Grapsidae	*Percnon*	*planissimum*	PEPL	100	37	2.1	1.3	2.1 – 19.2	0 – 98
Labridae	*Pseudocheilinus*	*tetrataenia*	PSTE	80	47	2.0	1.2	4.9 - 20.3	45 - 100
Hippolytidae	*Saron*	*marmoratus*	SAMA	80	37	2.0	1.6	2.1 – 15.5	50 - 100
Portunidae	*Charybdis*	*hawaiensis*	CHHA	80	47	1.9	1.1	2.1 – 25.3	50 - 98
Palaemonidae	*Palaemon*	*pacificus*	PAPA	60	32	1.5	1.1	2.1 – 13.4	20 - 100
Hippolytidae	*Saron*	*neglectus*	SANE	60	26	1.3	2.1	3.7 – 10.4	0 - 80
Cirrhitidae	*Cirrhitops*	*fasciatus*	CIFA	100	32	1.1	1	2.1 - 16.8	55 - 98

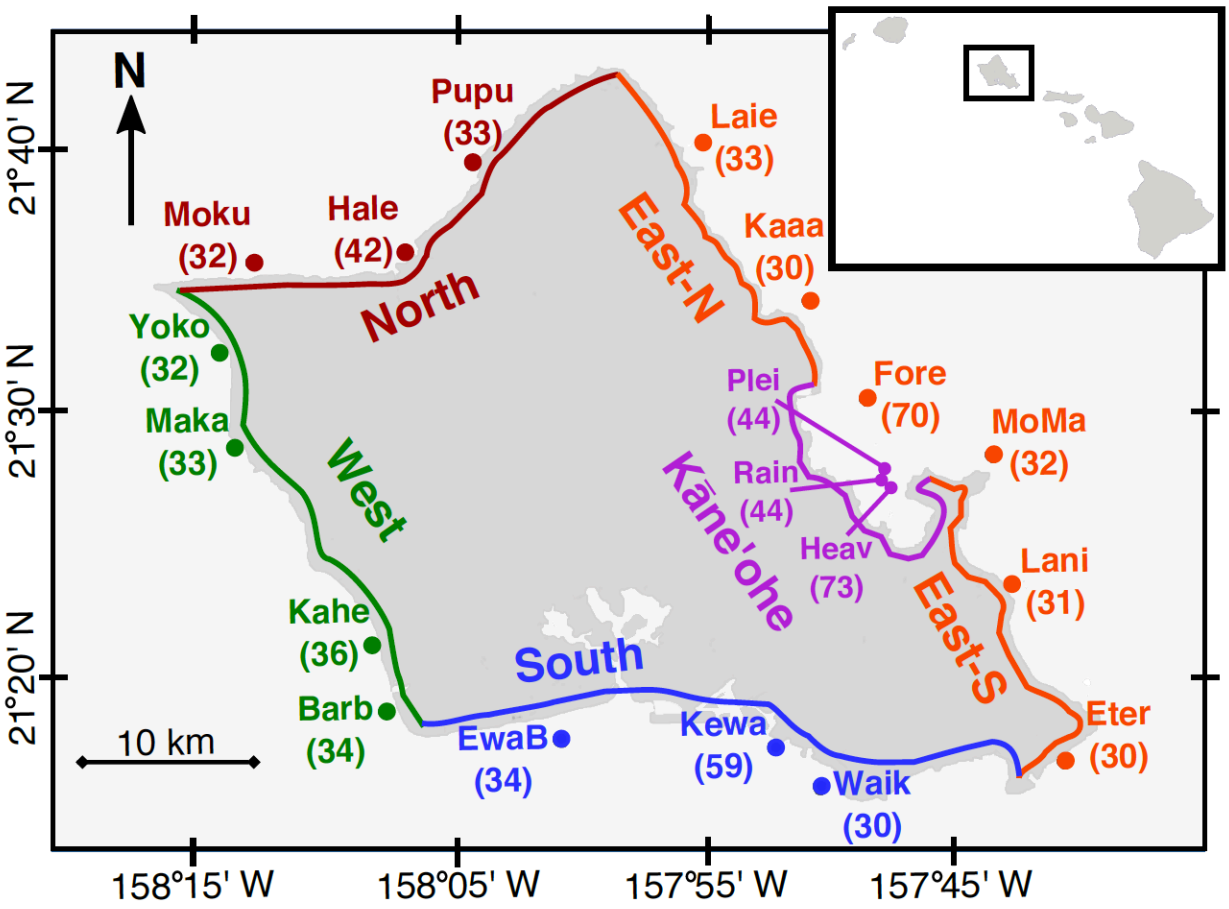

Figure 2.1. Location and name codes of 19 study sites around O‘ahu. For each site the number of colonies surveyed is given in parentheses. Sites are grouped by color into regions. Inset map of the main Hawaiian Islands with O‘ahu outlined. See Table 2.S4 for site names and coordinates.

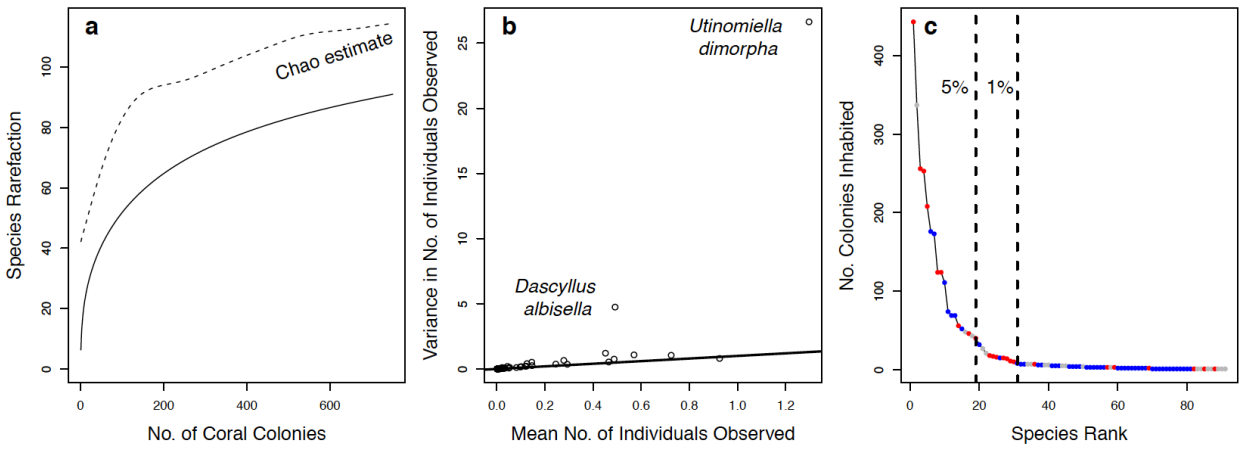

Figure 2.2. Characterization of community. (a) Species rarefaction curve for the overall pool of species found associated with 751 *Pocillopora meandrina*. The dashed line shows the mean Chao estimate for number of species, which reaches 115 species for 751 colonies. (b) For each of 91 species, the mean number of individuals observed and the variance in the number of individuals observed across colonies display a relative index of aggregation, where species that fall above the 1:1 line have clumped distributions. (c) Species rank abundance plot with decapods species shown in red, other invertebrates in grey, and fishes in blue. The dashed lines show cutoffs for species observed on 5% and 1% of colonies.

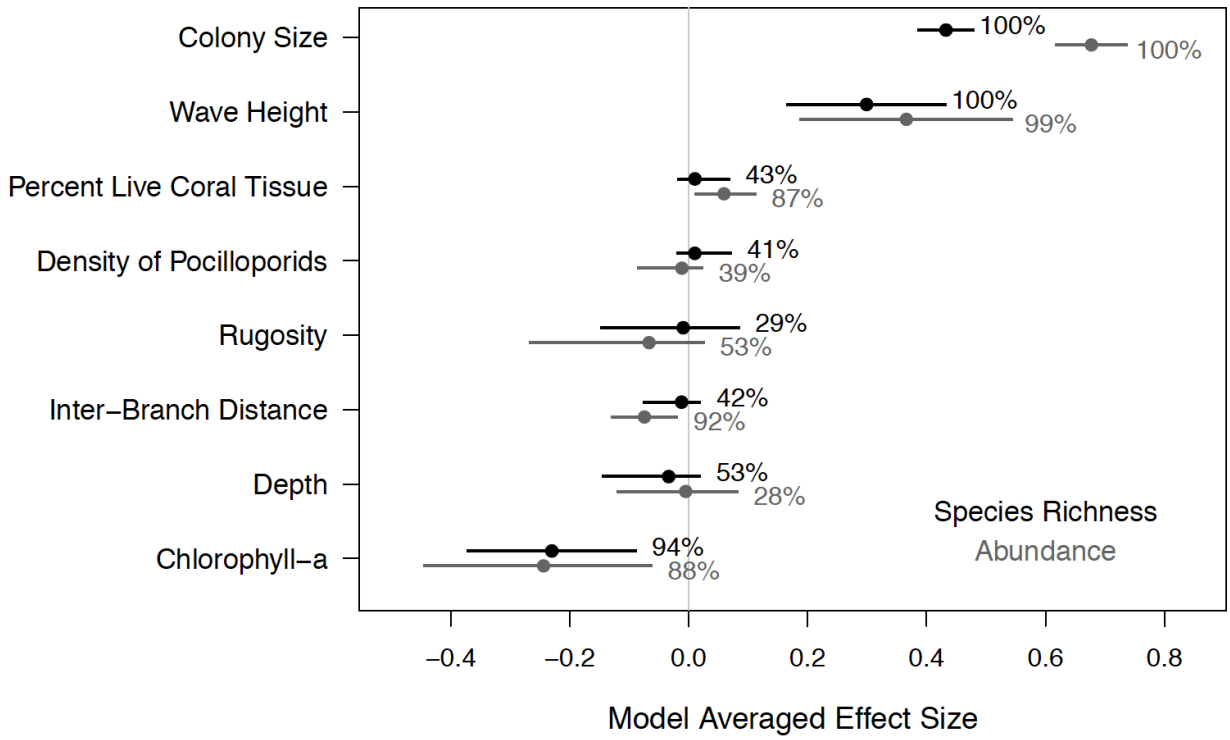

Figure 2.3. Multi-model-averaged parameter coefficients with 95% confidence intervals from the subset of models with ΔAIC <4 for each community metric, i.e., species richness (black, 31 models) and abundance (gray, 10 models). For the effect of a variable to be significantly different from zero, the error bars cannot overlap zero (thin vertical line), e.g., chlorophyll-a had a significant negative effect size for both abundance and species richness, however percent live coral tissue had a significant effect size only in relation to abundance. As a metric of relative model support, the summed model probabilities for the subset of models containing each parameter are listed.

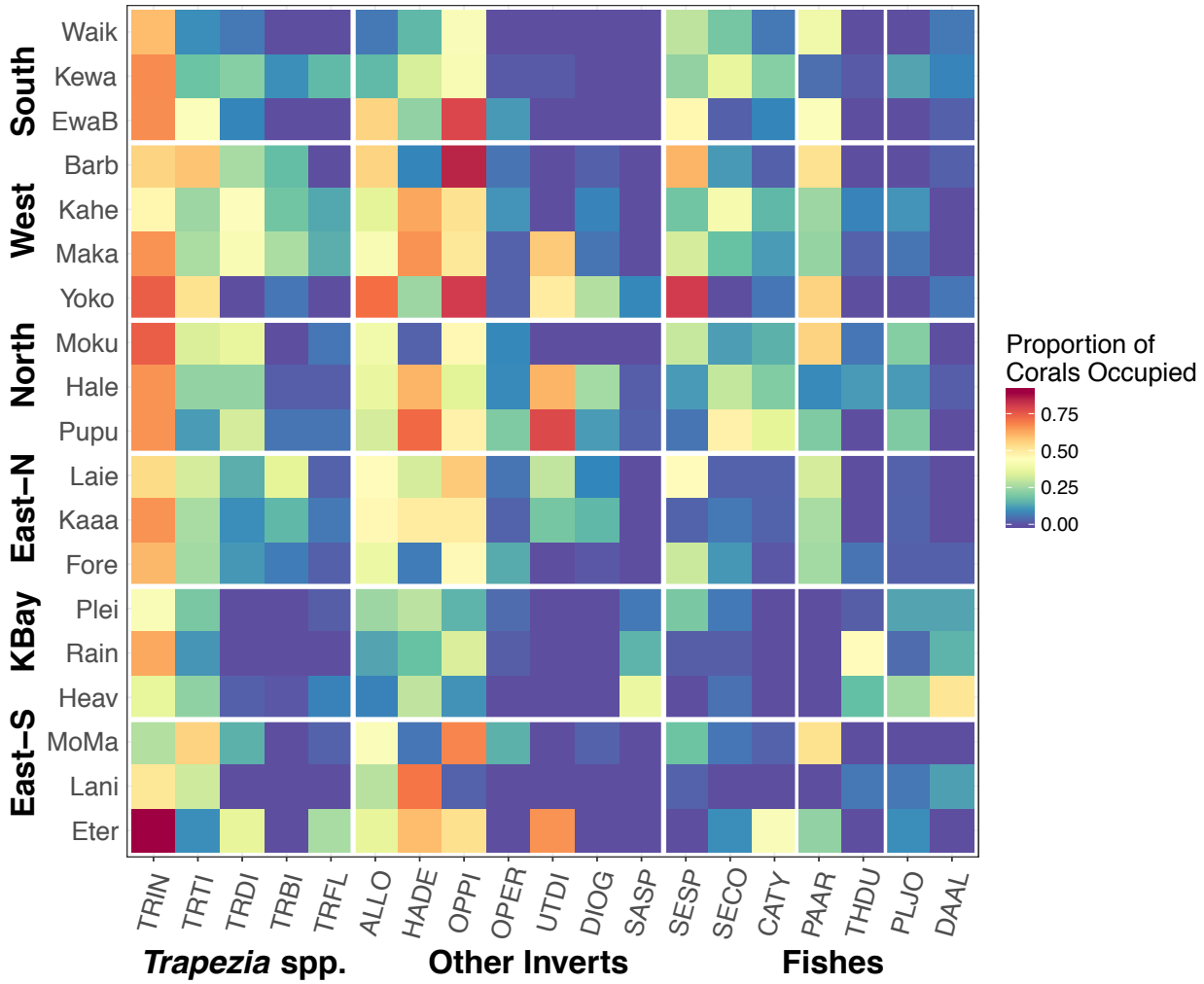

Figure 2.4. Heat map showing the proportion of colonies at a site (see Table 2.S4 for site details) inhabited by each species (see Table 2.2 for species names), calculated for the species observed on 5% or more of colonies (n=751). White horizontal lines divide the sites into regions. White vertical lines break the species into functional groups with fishes being further divided into: predatory fishes that live tucked in between the branches (left), other predatory fishes (middle), and planktivorous fishes (right).

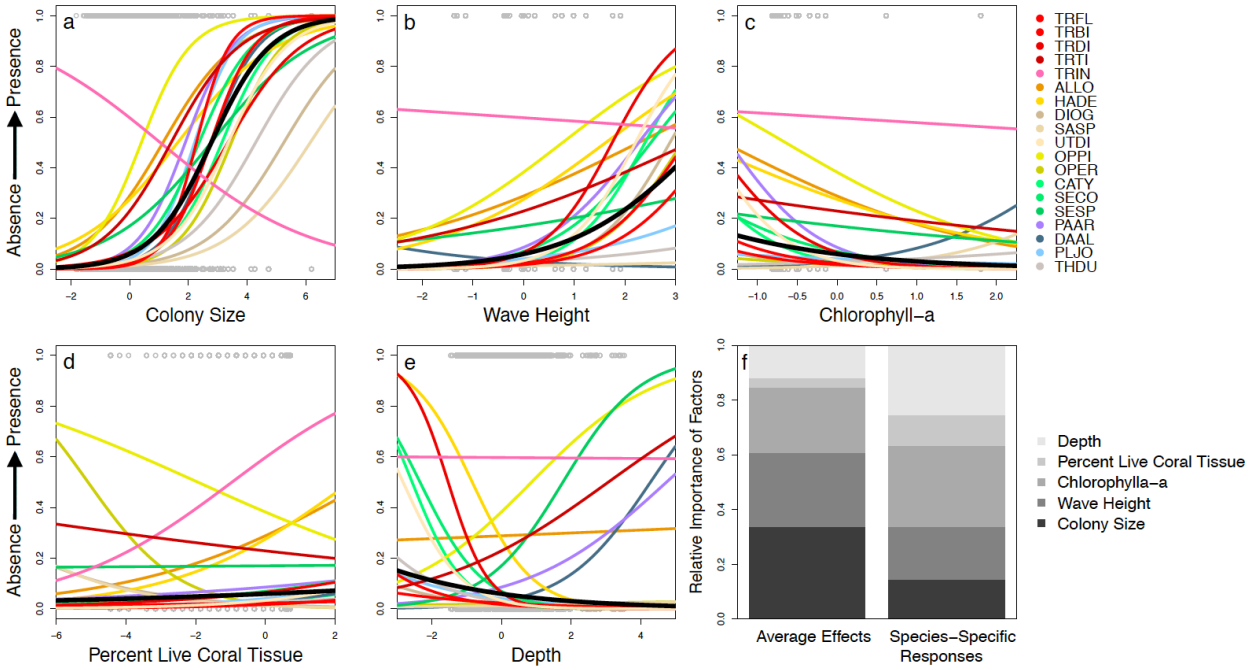

Figure 2.5. For a GLMM with species-specific responses to environmental gradients, sites, and regions (Model 2.S3), the species-specific probability of occurrence trends over environmental factors: (a) colony size, (b) wave height, (c) chlorophyll-a, (d) percent live coral tissue, and (e) depth are plotted with the average trend (across species) in black and data points in gray. See Table 2.2 for species codes. (f) The relative importance of each environmental factor based on average effects (fixed effect estimates) and species-specific responses (standard deviation of random effects).

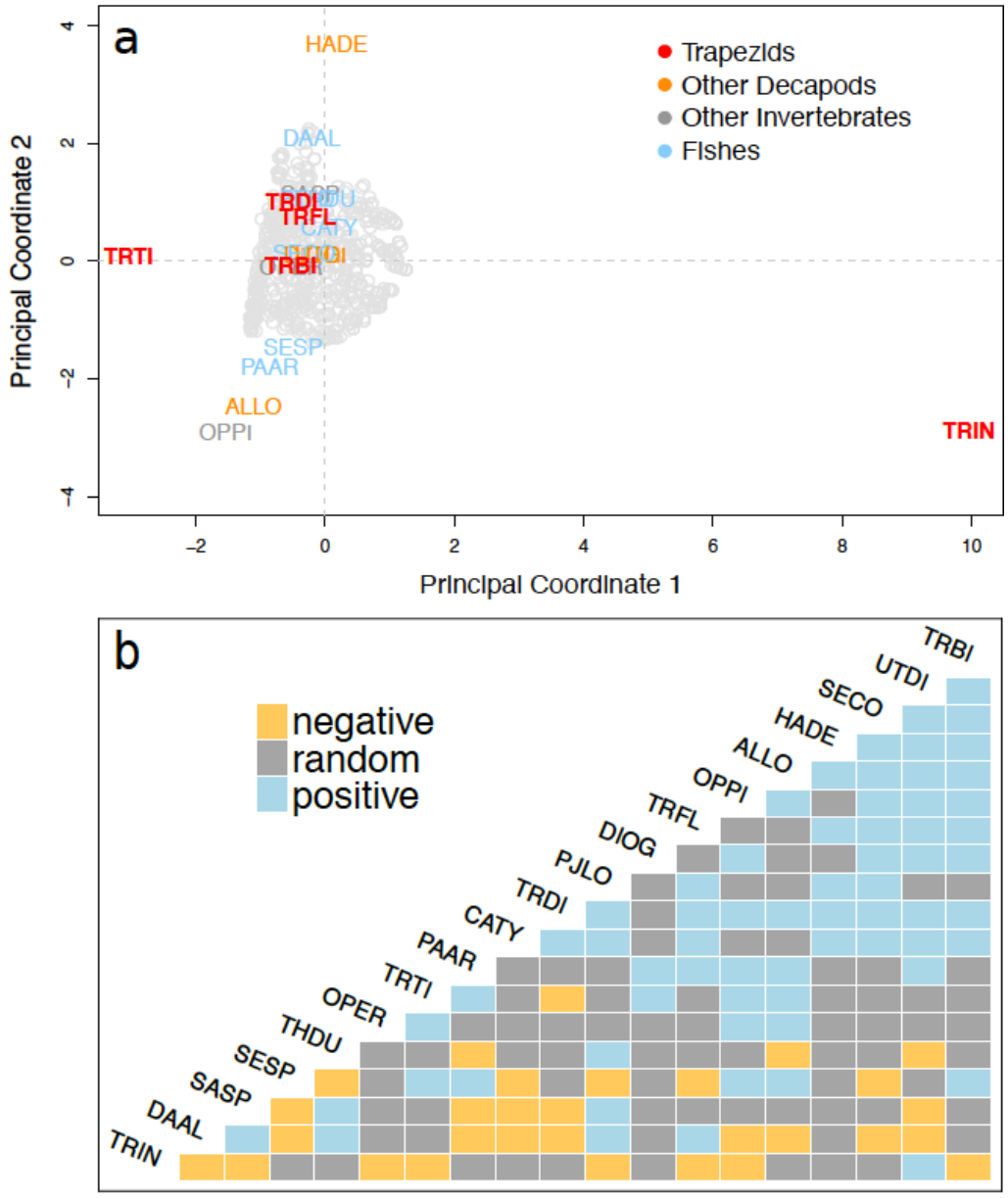

Figure 2.6. (a) The first two coordinates of a PCoA on community composition data for species observed on 5% or more of colonies (19 species, 751 colonies). *Trapezia intermedia* (TRIN) is the only species in the lower right quadrant. (b) Co-occurrence analysis depicts TRIN as being in 27% of negative co-occurrences (i.e., co-occurrences that were less frequent than expected given a random distribution of species). See Table 2.2 for species codes.

Table 2.S1. Correlation coefficients between environmental drivers measured at the colony and site scale; scores larger than ±0.5 listed in bold. Correlation scores for inter-branch distance and *Pocillopora* density are based on a subset of 708 colonies for which measurements of these variables were available. All other scores are based on 751 colonies.

Variable	Colony size	% Live	Inter-branch	Depth	Density of *Poc.*	Wave height	Rugosity	Chl-a
Colony size	1							
% Live tissue	-0.333	1						
Inter-branch distance	0.308	0.018	1					
Depth	-0.341	0.110	-0.056	1				
Density of *Poc.*	-0.131	0.185	0.011	-0.063	1			
Wave height	-0.411	0.176	-0.101	**0.534**	0.171	1		
Rugosity	-0.183	0.064	-0.080	**0.622**	0.017	0.411	1	
Chl-a	0.374	-0.214	0.150	**-0.603**	-0.256	**-0.595**	-0.399	1

Table 2.S2. Marginal R2 (variance explained by fixed effects) and conditional R2 (variance explained by full model including fixed and random effects) for a set of binomial GLMMs run with probability of occurrence for the species observed on ≥5% of colonies as the response variable.

Model set	$R^2_{marginal}$	$R^2_{conditional}$	**Fixed effects:** colony size, percent live coral tissue, depth, wave height, & chlorophyll-a	**Random effects:** species identity & colony nested in site nested in region	**Random effects:** species by site & species by region	**Random effects:** species-specific responses to fixed effects
Base model	------	0.3035		✔		
Compositional variation over spatial scales	------	0.5714		✔	✔	
Average environmental effects	0.0915	0.3251	✔	✔		
Average environmental effects & compositional variation over environmental factors	0.1297	0.6021	✔	✔		✔
Compositional variation over spatial scales & average environmental effects	0.0891	0.5832	✔	✔	✔	
Full model	0.1316	0.6822	✔	✔	✔	✔

Table 2.S3. Family, genus, species, % of regions, % of sites, % of colonies, average number of individuals observed on a colony, depth range, and % live coral tissue range listed for all fish (n=48) and invertebrate (n=43) species observed on 751 *Pocillopora meandrina*. *These rows are complexes of taxonomically similar species that were not consistently distinguishable in the field. *Sebastapistes* spp. includes observations of *S. fowleri*, *S. galactacma*, and *S. ballieui*.

Family	Genus	Species	% of regions	% of sites	% of colonies	Avg. per colony	Depth (m)	% live coral tissue
Acanthuridae	*Acanthurus*	*blochii*	20	5	0.1	1.0	16.2	95
Acanthuridae	*Acanthurus*	*triostegus*	40	16	0.5	1.8	1.5 – 2.7	45 - 100
Acanthuridae	*Ctenochaetus*	*strigosus*	20	5	0.1	1	2.4	30
Acanthuridae	*Zebrasoma*	*flavescens*	20	5	0.3	1.5	2.4 - 2.7	55 -95
Antennariidae	*Antennarius*	*commerson*	20	5	0.1	1	11.6	90
Apogonidae	*Pristiapogon*	*kallopterus*	20	5	0.1	1	2.1	85
Blenniidae	*Cirripectes*	*vanderbilti*	20	5	0.1	1	4.6	75
Blenniidae	*Exallias*	*brevis*	40	21	0.7	1	4.0 – 14.3	70 - 100
Caracanthidae	*Caracanthus*	*typicus*	80	79	9.9	1.5	2.4 – 16.8	50 - 100
Chaetodontidae	*Chaetodon*	*lunula*	20	11	0.5	2.3	14.3 – 20.4	40 - 80
Chaetodontidae	*Chaetodon*	*multicinctus*	20	5	0.1	1	3.7	75
Cirrhitidae	*Amblycirrhitus*	*bimacula*	100	42	4.3	1.2	3.0 - 14.3	0 - 100
Cirrhitidae	*Cirrhitops*	*fasciatus*	100	32	1.1	1	2.1 - 16.8	55 - 98
Cirrhitidae	*Paracirrhites*	*arcatus*	80	79	23.0	1.3	3.4 – 31.1	0 - 100
Cirrhitidae	*Paracirrhites*	*forsteri*	60	16	0.4	1	2.4 – 11.6	90 - 95
Gobiidae	*Asterropteryx*	*semipunctatus*	20	11	0.4	1	2.1 - 2.7	30 - 95
Gobiidae	*Eviota*	*susanae*	20	11	0.4	1.3	2.4 - 2.7	30 - 70
Labridae	*Coris*	*venusta*	20	5	0.5	1	2.1	60 - 95
Labridae	*Gomphosus*	*varius*	20	5	0.3	1	2.7	90 - 95
Labridae	*Novaculichthys*	*taeniourus*	60	16	0.8	1.2	6.7 - 30.8	0 - 100
Labridae	*Pseudocheilinus*	*octotaenia*	20	5	0.1	1	15.5	80
Labridae	*Pseudocheilinus*	*tetrataenia*	80	47	2.0	1.2	4.9 - 20.3	45 - 100
Labridae	*Stethojulis*	*balteata*	40	16	0.5	1	2.1 – 26.2	20 - 90
Labridae	*Thalassoma*	*ballieui*	20	5	0.1	1	2.1	90
Labridae	*Thalassoma*	*duperrey*	100	53	6.9	1.4	2.1 – 20.1	5 - 100
Lutjanidae	*Lutjanus*	*kasmira*	20	5	0.3	1.5	18.0	0 - 60
Monacanthidae	*Cantherhines*	*verecundus*	20	11	0.4	1	11.9 – 18.0	0 - 95
Mullidae	*Parupeneus*	*pleurostigma*	20	5	0.3	1	2.4	90 - 95
Muraenidae	*Gymnomuraena*	*zebra*	20	5	0.1	1	5.8	95
Muraenidae	*Gymnothorax*	*melatremus*	20	11	0.3	1	10.7 – 18.3	30 - 55
Muraenidae	*Gymnothorax*	*undulatus*	40	11	0.3	1	2.7 – 9.1	55 - 90
Ostraciidae	*Ostracion*	*meleagris*	20	5	0.3	1	2.4	30 - 65

Table 2.S3. (Continued) Family, genus, species, % of regions, % of sites, % of colonies, average number of individuals observed on a colony, depth range, and % live coral tissue range listed for all fish (n=48) and invertebrate (n=43) species observed on 751 *Pocillopora meandrina*.

Family	Genus	Species	% of regions	% of sites	% of colonies	Avg. per colony	Depth (m)	% live coral tissue
Pomacentridae	*Centropyge*	*potteri*	20	5	0.3	1	15.8 – 25.9	80 - 95
Pomacentridae	*Chromis*	*vanderbilti*	60	21	0.7	1.6	5.8 – 20.1	95 - 100
Pomacentridae	*Dascyllus*	*albisella*	100	58	9.2	5.3	1.5 – 30.2	0 - 100
Pomacentridae	*Plectroglyphididon*	*johnstonianus*	100	74	9.2	1.3	2.1 – 26.2	0 - 100
Priacanthidae	*Heteropriacanthus*	*cruentatus*	40	11	0.4	1	2.1 – 7.0	60 - 90
Scaridae	*Chlorurus*	*spilurus*	20	5	0.3	1	2.4	90 - 95
Scaridae	*Scarus*	*psittacus*	20	16	0.8	2.7	2.1 – 3.4	30 – 90
Scorpaenidae	*Dendrochirus*	*barberi*	60	21	0.9	1	2.1 – 18.3	30 – 90
Scorpaenidae	*Pterois*	*sphex*	20	5	0.1	3	14.3	75
Scorpaenidae	*Scorpaenopsis*	*diabolus*	20	5	0.1	1	13.4	100
Scorpaenidae	*Sebastapistes*	*coniorta*	100	89	15	1.9	2.1 – 19.5	30 - 100
*Scorpaenidae	*Sebastapistes*	spp.	100	89	23	1.9	2.4 – 30.5	30 - 100
Tetraodontidae	*Canthigaster*	*amboinensis*	20	5	0.1	1	7.3	95
Tetraodontidae	*Canthigaster*	*coronata*	40	16	0.4	1	10.7 – 14.3	55 - 100
Tetraodontidae	*Canthigaster*	*jactator*	80	37	0.9	1.3	2.1 – 17.1	60 - 100
Zanclidae	*Zanclus*	*cornutus*	20	5	0.7	1.6	2.1 – 2.4	30 - 90
Alpheidae	*Alpheus*	*lottini*	100	100	33.7	1.4	0.6 – 26.8	30 - 100
Alpheidae	*Alpheus*	*pacificus*	40	16	0.4	1	2.1 – 11.6	50 - 90
Amphinomidae	*Pherecardia*	*striata*	20	5	0.1	1	7.3	70
Carpiliidae	*Carpilius*	*convexus*	20	5	0.1	1	2.4	90
Chromodorididae	*Thorunna*	*kahuna*	20	5	0.1	1	2.7	45
Cidaridae	*Chondrocidaris*	*gigantea*	40	16	0.7	1.6	12.8 – 26.2	0 - 90
Cidaridae	*Eucidaris*	*metularia*	80	26	0.9	1.3	4.3 – 20.1	0 - 95
Cryptochiridae	*Utinomiella*	*dimorpha*	80	42	16.5	7.9	3.0 - 18.3	30 - 100
Diadematidae	*Echinothrix*	*calamaris*	60	21	0.9	1.1	2.1 – 15.8	30 - 100
Diadematidae	*Echinothrix*	*diadema*	40	21	0.8	1	10.4 – 15.5	55 - 100
*Paguroidea	unidentified		60	53	5.3	2.4	2.4 – 19.8	0 - 100
Domeciidae	*Domecia*	*hispida*	80	47	2.4	1.4	3.4 – 19.8	40 - 100
Echinometridae	*Echinometra*	*mathaei*	80	53	3.6	1.5	4.3 – 29.6	0 - 100
Echinometridae	*Heterocentrotus*	*mamillatus*	60	21	0.5	1	4.3 – 14.9	0 - 100
Grapsidae	*Percnon*	*affine*	20	5	0.1	1	2.4	90
Grapsidae	*Percnon*	*planissimum*	100	37	2.1	1.3	2.1 – 19.2	0 - 98
Hippolytidae	*Saron*	*marmoratus*	80	37	2.0	1.6	2.1 – 15.5	50 - 100

Table 2.S3. (Continued) Family, genus, species, % of regions, % of sites, % of colonies, average number of individuals observed on a colony, depth range, and % live coral tissue range listed for all fish (n=48) and invertebrate (n=43) species observed on 751 *Pocillopora meandrina*.

Family	Genus	Species	% of regions	% of sites	% of colonies	Avg. per colony	Depth (m)	% live coral tissue
Hippolytidae	*Saron*	*neglectus*	60	26	1.3	2.1	3.7 – 10.4	0 - 80
Hymenoceridae	*Hymenocerca*	*picta*	20	5	0.1	3	11.6	95
*Muricidae	*Drupella*	spp.	60	16	0.8	2	11.6 - 20.1	0 - 95
Muricidae	*Quoyula*	*monodonta*	80	42	2.8	1.6	2.7 – 17.7	50 - 100
Ophidiasteridae	*Linckia*	*multifora*	20	5	0.1	1	15.8	85
Ophiocomidae	*Ophiocoma*	*erinaceus*	100	79	6.4	1.3	2.7 – 20.4	0 - 100
Ophiocomidae	*Ophiocoma*	*pica*	100	100	45	1.6	1.5 – 30.5	0 - 100
Palaemonidae	*Harpiliopsis*	*depressa*	100	100	34.1	1.7	0.9 – 24.7	0 - 100
Palaemonidae	*Palaemon*	*pacificus*	60	32	1.5	1.1	2.1 – 13.4	20 - 100
Portunidae	*Charybdis*	*hawaiensis*	80	47	1.9	1.1	2.1 – 25.3	50 - 98
Portunidae	*Thalamita*	*coerulipes*	40	16	0.4	1	1.8 - 2.7	60 – 90
Sabellidae	*Sabellastarte*	*spectabilis*	60	32	5.7	2.5	2.1 – 18.3	0 - 100
Sepiolidae	*Euprymna*	*scolopes*	20	5	0.1	1	12.8	50
*Serpulidae	*Spirobranchus*	spp.	60	21	0.7	1.4	12.5 – 16.8	80 - 100
Stenopodidae	*Stenopus*	*hispidus*	60	21	0.9	1.4	2.1 – 18.3	0 - 100
Stomatopoda	*Gonodactylaceus*	*falcatus*	40	11	0.4	1	2.4 – 15.5	65 - 99
Terebellidae	*Loimia*	*medusa*	20	5	0.1	1	2.7	10
Terebridae	*Terebra*	*gouldi*	20	5	0.1	1	2.7	45
Trapeziidae	*Trapezia*	*bidentata*	100	58	7.5	1.6	2.1 – 18.0	45 - 100
Trapeziidae	*Trapezia*	*digitalis*	100	79	16.5	1.5	2.1 – 19.5	45 - 100
Trapeziidae	*Trapezia*	*flavopunctata*	100	68	6.1	1.7	2.1 – 16.8	50 - 100
Trapeziidae	*Trapezia*	*intermedia*	100	100	59.0	1.6	0.6 - 31.1	20 - 100
Trapeziidae	*Trapezia*	*tigrina*	100	100	27.7	1.8	1.5 – 26.2	30 - 100
*Vermetidae	unidentified		20	5	0.1	1	2.7	50
Xanthidae	*Liomera*	*rubra*	40	11	0.3	1.5	9.1 – 18.0	0 - 100
Xanthidae	*Pseudoliomera*	*speciosa*	100	68	2.3	1.4	2.1 – 14.3	75 - 100

Table 2.S4. List of site names, abbreviations, coordinates, regions, and depth ranges for 19 survey sites around O‘ahu, Hawai‘i.

Site name	Code	Latitude	Longitude	Region	Depth (m)
Heaven	Heav	21.4516	-157.7904	Kāne’ohe	2.1 – 2.4
Pleiades	Plei	21.4564	-157.7945	Kāne’ohe	2.4 – 3.7
Rainbow	Rain	21.4549	-157.7947	Kāne’ohe	2.4 – 3.0
La‘ie	Laie	21.6636	-157.9155	East	11.9 – 14.3
Ka’a’awa	Kaaa	21.5664	-157.8436	East	11.0 – 13.4
Kāne‘ohe Forereef	Fore	21.5087	-157.8051	East	9.4 – 30.5
Moku Manu	MoMa	21.4710	-157.7209	East	15.2 – 20.7
Lanikai	Lani	21.3906	-157.7086	East	0.6 – 2.7
Eternity Beach	Eter	21.2812	-157.6766	East	7.3 – 10.4
Waikīkī	Waik	21.2687	-157.8378	South	7.9 - 15.8
Kewalo	Kewa	21.2904	-157.8655	South	6.1 – 17.7
‘Ewa Beach	EwaB	21.2930	-158.0102	South	12.2 - 16.2
Barber's Point	Barb	21.3112	-158.1276	West	9.8 – 25.0
Kahe Point	Kahe	21.3528	-158.1318	West	3.4 – 7.0
Mākaha	Maka	21.4748	-158.2267	West	3.7 – 14.0
Yokohama	Yoko	21.5339	-158.2348	West	13.7 – 18.3
Hale‘iwa	Hale	21.5955	-158.1105	North	2.4 – 8.5
Pupukea	Pupu	21.6521	-158.0634	North	5.8 – 10.4
Mokulē‘ia	Moku	21.5910	-158.2153	North	10.7 – 20.1

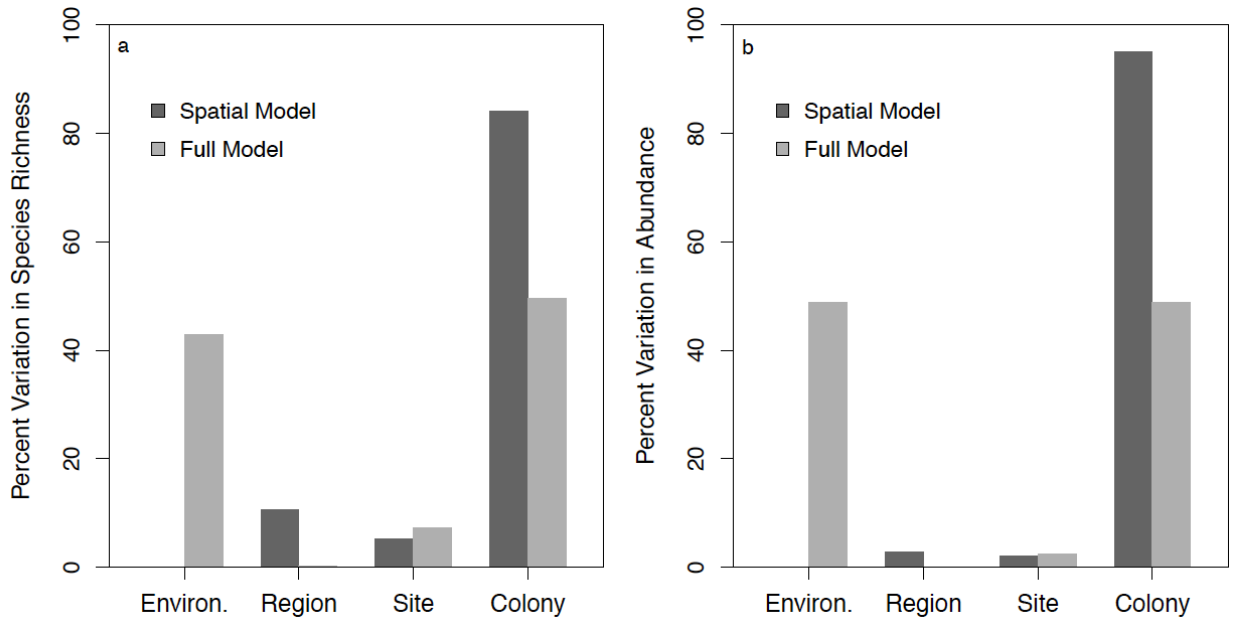

Figure 2.S1. Paired barplot for percent variation in species richness (a) and community abundance (b) of coral-associated communities (n=708) across spatial scales and environmental factors. Dark gray bars are from a model that included only spatial scales (Model 2.S1). Light gray bars are from a model that also included environmental factors (Model 2.S2).

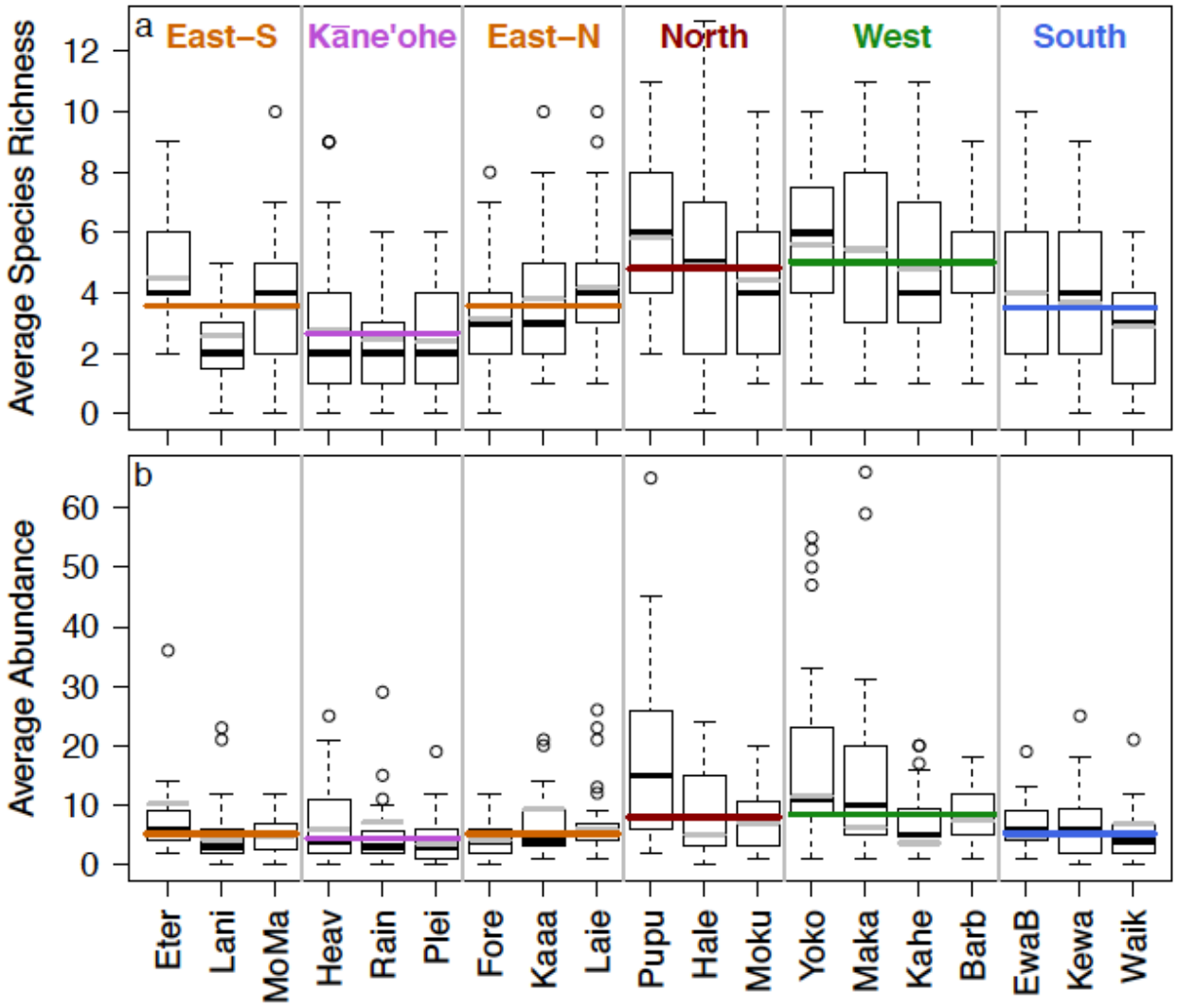

Figure 2.S2. Mean species richness (a) and community abundance (b) per colony by site, vertical gray lines separating regions. Model estimates of region means are displayed with colored line segments. Within the 25 to 75% quantile box, the light gray horizontal line segments correspond to the model estimates of site means, and the black line segments correspond to the 50% quantile for each site. See Table 2.S4 for site coordinates.

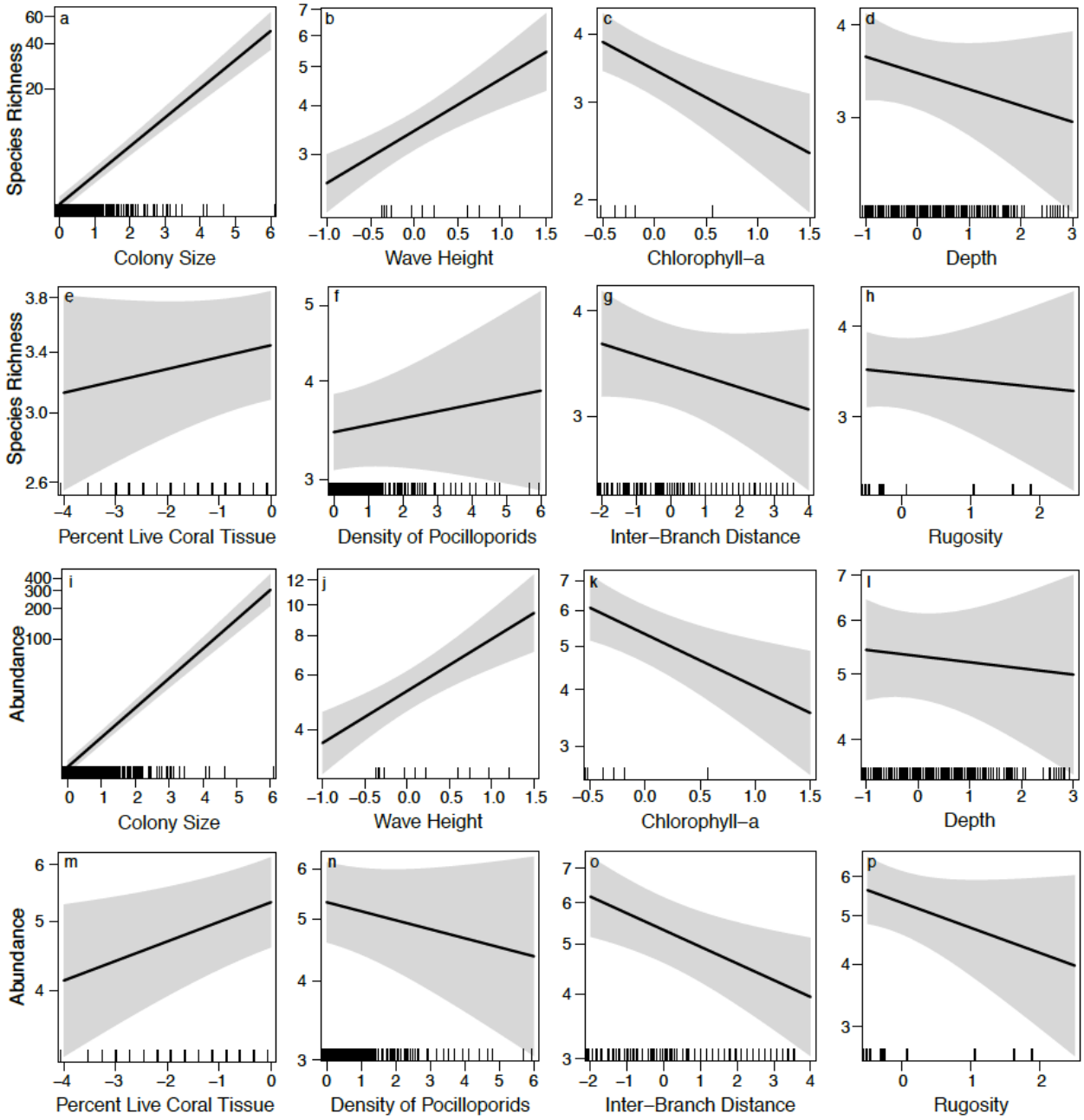

Figure 2.S3. Plots of the average effect (across regions and sites) of environmental factors from GLMMs (Model 2.S2) with species richness (a-h) and community abundance (i-p) as the response variables. Gray bars show the 95% confidence interval on model estimates.

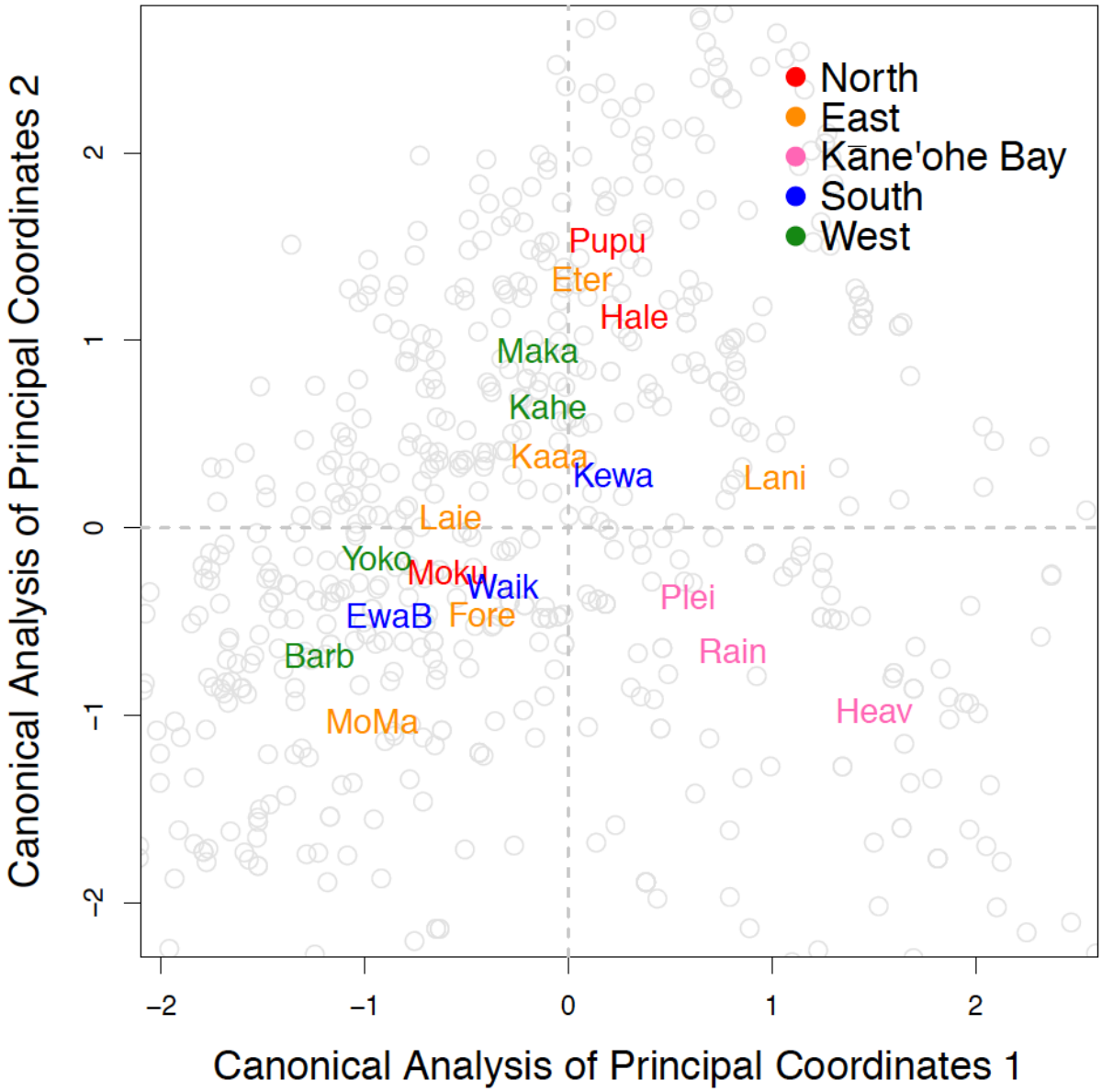

Figure 2.S4. Canonical analysis of principal coordinates constrained by sites (in *R*, function "capscale" in package *vegan*; Oksanen et al. 2017) estimates how much variation in the community composition was explained by variation at the site scale (18%). Sites are shown at their centroids with site codes (see Table 2.S4 for site names).

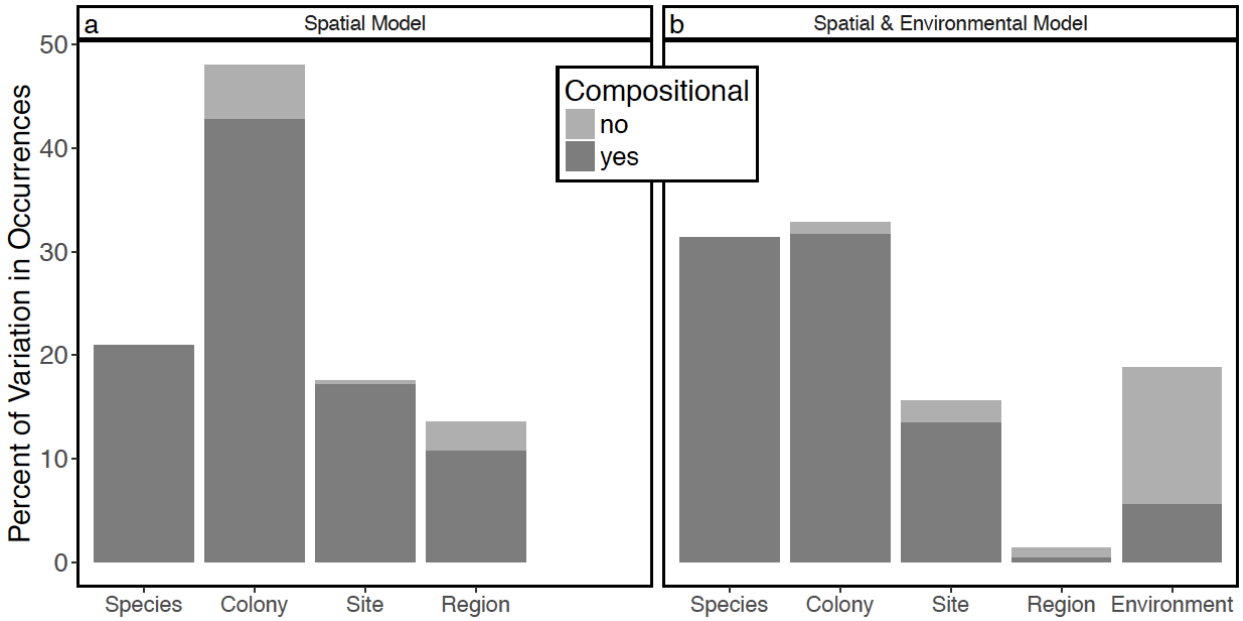

Figure 2.S5. Variance in occurrences partitioned across spatial scales based on random effect estimates from a spatial GLMM with occurrence as the response variable, survey structure and species-specific spatial patterns included as random effects (a); and an environmental and spatial GLMM with average and species-specific responses to environmental factors added to the components of the spatial model (b). These models correspond to the "Compositional variation over spatial scales" model (a) and the "Full model" (b, Model 2.S3) in Table 2.S2.

Model 2.S1. For the community metrics the model with only random effects was:

$$Y_{ijk} \sim Poisson(\lambda_{ijk})$$

$$\log(\lambda_{ijk}) = \beta_0 + \alpha_k + \eta_{jk} + \varepsilon_{ijk}$$

$$\alpha_k \sim Normal(0, \sigma_{region})$$

$$\eta_{jk} \sim Normal(0, \sigma_{site})$$

$$\varepsilon_{ijk} \sim Normal(0, \sigma_{colony})$$

where Y_{ijk} is community abundance or species richness of colony *i* at site *j* in region *k*, λ_{ijk} is the community metric at colony *i* in site *j* in region *k*, α_k is the random effect for region *k*, normally distributed with mean zero and standard deviation σ_{region}, η_{jk} is the random effect for site *j* in region *k*, normally distributed with mean zero and standard deviation σ_{site}, ε_{ijk} is the random effect for colony *i* in site *j* in region *k*, normally distributed with mean zero and standard deviation σ_{colony}, and β_0 is the overall mean community metric across samples.

R code for this model: glmer(community_metric ~ (1|Colony)) + (1|Site) + (1|Region), data=oahu_commonspecies, family=poisson)

Model 2.S2. For the community metrics, the model with fixed and random effects was:

$$Y_{ijk} \sim Poisson(\lambda_{ijk})$$

$$\begin{aligned}\log(\lambda_{ijk}) = {} & \beta_0 + \alpha_k + \eta_{jk} + \varepsilon_{ijk} + \beta_1 \times depth_i + \beta_2 \times percent\_live\_coral\_tissue_i \\ & + \beta_3 \times colony\_size_i + \beta_4 \times density\_of\_Pocillopora_i \\ & + \beta_5 \times branch\_distance_i + \beta_6 \times wave\_height_j + \beta_7 \times rugosity_j \\ & + \beta_8 \times chlorophyll\_a_j\end{aligned}$$

$$\alpha_k \sim Normal(0, \sigma_{region})$$

$$\eta_{jk} \sim Normal(0, \sigma_{site})$$

$$\varepsilon_{ijk} \sim Normal(0, \sigma_{colony})$$

where Y_{ijk} is community abundance or species richness of colony *i* at site *j* in region *k*, λ_{ijk} is the mean community metric at colony *i* in site *j* in region *k*, α_k is the random effect for region *k*,

normally distributed with mean zero and standard deviation σ_{region}, η_{jk} is the random effect for site *j* in region *k*, normally distributed with mean zero and standard deviation σ_{site}, ε_{ijk} is the random effect for colony *i* in site *j* in region *k*, normally distributed with mean zero and standard deviation σ_{colony}, and β_0 is the overall mean community metric across samples.

R code for this model: glmer(community_metric ~ depth + percent_live_coral_tissue + colony_size + density_of_Pocillopora + branch_distance + wave_height + rugosity + chlorophyll_a + (1|Colony) + (1|Site) + (1|Region), data=common_species, family=poisson)

Model 2.S3. For community composition, the full model (Table 2: Model 4) was:

$$Y_{ijk}^{n} \sim Bernoulli\left(p_{ijk}^{n}\right)$$

$$\text{logit}\left(p_{ijk}^{n}\right) =$$

$$\beta_{0,ijk}^{n} + \beta_{1}^{n} \times depth_i + \beta_{2}^{n} \times percent\_live\_coral\_tissue_i + \beta_{3}^{n} \times colony\_size_i +$$

$$\beta_{4}^{n} \times wave\_height_j + \beta_{5}^{n} \times chlorophyll\_a_j$$

$$\beta_{0,ijk}^{n} = \overline{\beta_0} + \varepsilon_i + \eta_j + \alpha_k + \delta^n + \varphi_j^n + \kappa_k^n$$

$$\varepsilon_i \sim Normal(0, \sigma_{coral});\ \eta_j \sim Normal(0, \sigma_{site});\ \alpha_k \sim Normal\left(0, \sigma_{region}\right);\ \delta^n \sim Normal\left(0, \sigma_{species}\right);$$

$$\varphi_j^n \sim Normal\left(0, \sigma_{site:species}\right);\ \kappa_k^n \sim Normal\left(0, \sigma_{region:species}\right)$$

$$\beta_1^n = \overline{\beta_1} + b_1^n;\ b_1^n \sim Normal(0, \sigma_{depth})$$

$$\beta_2^n = \overline{\beta_2} + b_2^n;\ b_2^n \sim Normal\left(0, \sigma_{percent\_live\_coral\_tissue}\right)$$

$$\beta_3^n = \overline{\beta_3} + b_3^n;\ b_3^n \sim Normal\left(0, \sigma_{colony\_size}\right)$$

$$\beta_4^n = \overline{\beta_4} + b_4^n;\ b_4^n \sim Normal\left(0, \sigma_{wave\_height}\right)$$

$$\beta_5^n = \overline{\beta_5} + b_5^n;\ b_5^n \sim Normal(0, \sigma_{chlorophyll\_a})$$

where p_{ijk}^{n} is the probability of observing species *n* on colony *i* at site *j* in region *k*, Y_{ijk}^{n} is the estimated probability of observing species *n* on colony *i* at site *j* in region *k*, $\overline{\beta_0}$ is the overall mean probability of occurrence, ε_i is the random effect for colony *i*, η_j is the random effect for site *j*, α_k is the random effect for region *k*, δ^n is the random effect for species *n*, φ_j^n is the

random effect for species n at site *j*, κ_k^n is the random effect for species *n* at region *k*, each random effect is normally distributed with mean zero and a unique (for each random effect) standard deviation σ, residual variance in this model is at the scale of colony:species. This model is analogous to a constrained ordination, but uses a full statistical model and allows for hierarchical random variation.

R code for this model: glmer(presence_absence ~ depth + percent_live_coral_tissue + colony_size + wave_height + chlorophyll_a + (1|Colony) + (1|Site) + (1|Region) + (1 + depth + percent_live_coral_tissue + colony_size + wave_height + chlorophyll_a |species) + (1|Site:species) + (1|Region:species), data=really_common_species, family=binomial)

CHAPTER 3

Species sorting drives temporal variation in the composition of coral-associated metacommunities

Abstract

Temporal patterns in community composition can help disentangle the effects of the multiple underlying processes that structure communities. In this study, we compared spatial and temporal variation in the composition of communities associated with discrete habitat patches formed by a branching coral, *Pocillopora meandrina*. We surveyed the communities associated with 42 focal coral colonies at two sites (one within a bay and one on a forereef) approximately monthly from June 2014 to November 2017 (42 months), conducting a total of 1,437 community surveys. Following the community on a single colony through time, the community composition diverged from earlier versions asymptotically with increasing temporal distance. Within-colony temporal community dissimilarity was not predicted to exceed between colony dissimilarity, even with multiple years between surveys. Following within-colony species-specific patterns through time, 34 species (from 61 observed species) had stronger site-attachment on individual host colonies than expected given a random distribution across colonies, which included 25 species with unknown effects on the growth and survival of the host coral. Temporal variation in biophysical environmental parameters was not strongly associated with variation in community composition or diversity metrics. However, there was a positive effect of increasing wave energy on average species richness at the forereef site, and a negative effect of increasing temperature on average community dissimilarity at the bay site. Transition probability models illuminated species-specific positive and negative effects on arrival and persistence dynamics among both trapeziid crab species and Scorpaenidae fishes. Overall, our results showed strong evidence for niche-based processes (i.e., species sorting for fitness optimization as a result of abiotic and biotic factors at the habitat patch scale) as the main mechanisms structuring coral-associated reef communities. This included significant effects of species presence on the arrival and persistence of other species, high colony-scale variation in within-colony dissimilarity dynamics over time, significant associations between colony characteristics and community composition, and high unexplained colony-scale variation in community diversity metrics even after accounting for

measured colony parameters. This research characterizes patch- and metacommunity-scale temporal patterns in coral-associated communities, emphasizes the importance of species sorting dynamics for these communities, and outlines a template for temporal community analyses.

Introduction

A fundamental goal of community ecology is to understand the relative importance of various mechanisms driving variation in community composition. For communities associated with fairly discrete habitat patches that are connected by dispersal (i.e., metacommunities), patch habitat quality (species sorting), within patch species interactions (patch dynamics), migration between patches (mass effects), and a null model of stochastic processes (neutral dynamics) have been presented as structuring paradigms (Leibold et al. 2004). These paradigms are not mutually exclusive, but can lead to different predictions about patterns in community composition. For example, if species sort to different habitat patches based on species-specific metrics of habitat quality, similar community compositions would be expected between patches with similar habitat qualities (Cottenie 2005; Paradise et al. 2008; Macneil et al. 2009; Silva et al. 2018). For metacommunities structured primarily by the dynamics of species interactions within patch habitats, non-random co-occurrence patterns reflecting competitive exclusion and predator-prey interactions are expected (Connell 1961; Sutherland 1974; Palmer et al. 2002; Litvinov et al. 2007; Stier et al. 2013; Stier and Leray 2014). Species sorting based on patch habitat quality and patch dynamics resulting from species interactions are both niche-based community assembly processes.

Community assembly processes that are not necessarily associated with fundamental niches of species include connectivity (e.g., emigration between patches) and stochastic variation (e.g., growth and survival rates of individuals). Connectivity barriers can influence emigration among habitat patches and across regions, thereby affecting the arrival of species to habitat patches. Barriers to connectivity can include physical isolation or areas of unsuitable habitat (Kalmar and Currie 2006; Burns et al. 2010), as well as biophysical parameters, e.g., oceanographic currents (Basterretxea et al. 2013) and eddies (Fox et al. 2012). Regional gradients in biophysical parameters can drive variation in community composition at the patch

scale through differential species-specific connectivity dynamics (Cornell and Karlson 2000; Silva et al. 2018). For communities with high levels of connectivity, emigration between patches should result in well-mixed community composition across patches despite habitat heterogeneity (Leibold et al. 2004). In addition to directly limiting connectivity between patches or sites, regional biophysical parameters can structure communities through environmental filtering on species arrival, i.e., community formation, and/or species persistence, i.e., community maintenance. If biophysical parameters influence community maintenance as well as community formation, community composition should fluctuate with these environmental variables through time (Anderson et al. 2011; Freestone and Inouye 2015; Fitzgerald et al. 2017). The final paradigm in which community composition is primarily structured by stochastic processes is considered a null model of neutral metacommunity dynamics (Chave 2004; Leibold et al. 2004; Hubbell 2005). This null model considers species to be ecologically equivalent, exhibiting extinction and migration dynamics based on stochastic vital rates of individuals. For a community structured by stochastic process, species would not have consistent interaction dynamics with other species or associations with particular patches based on habitat quality.

Spatial patterns can illustrate how community composition varies along environmental gradients at the regional and patch scales, in addition to highlighting non-random distribution patterns between species pairs (Counsell et al. 2018). However, spatial surveys provide only a snapshot of communities and often cannot resolve competing mechanistic hypotheses. For example, spatial patterns can suggest how common or rare species are within a community, but cannot elucidate the transient or resident nature of species associations with habitat patches or the overall temporal consistency of a community. Spatial surveys can provide evidence of shifts in the composition of communities along regional biophysical gradients; however, they cannot disentangle whether these drivers are affecting community formation and/or maintenance dynamics. In addition, non-random co-occurrence patterns can be the result of multiple underlying community assembly processes. This includes environmental filtering over regional biophysical parameters or differences in patch habitat quality, species-specific responses to connectivity barriers, or species interactions. For example, negative co-occurrence patterns between two species may arise due to competitive exclusion (species interactions) or differences in habitat preference (species sorting). Alternatively, positive co-occurrence patterns between

two species could be evidence of similar habitat preferences (species sorting), species facilitation dynamics (positive species interactions), or ongoing competition for resources (non-equilibrium negative species interactions) (Barner et al. 2018).

Temporal patterns of community composition can strengthen evidence for the potential mechanisms structuring communities and can help disentangle the influence of multiple underlying processes (Freestone and Inouye 2015). Following the composition of communities through temporal shifts in biophysical parameters can distinguish whether these drivers are influencing community maintenance (the persistence of species within communities) or community formation (the ability of species to successfully arrive at habitat patches). For biophysical parameters that are associated with regional variation in community composition but not temporal variation (e.g., elevational gradients, Silva et al. 2018), these parameters are likely influencing community formation either through connectivity dynamics or environmental filtering. If variation in community composition through time is associated with biophysical parameters, these factors are likely affecting community maintenance through environmental filtering, e.g., seasonal shifts (Fitzgerald et al. 2017). When community composition varies along biophysical gradients over spatial and temporal scales, these factors are likely influencing both the formation and maintenance components of community assembly (Freestone and Inouye 2015). Further, surveys of communities through time enable comparison of the effects of environmental filtering at regional and habitat patch scales through analyses of temporal variation in community composition within and between habitat patches. Temporal dynamics can also refine competing hypotheses for mechanisms driving non-random species co-occurrences: the effect of a species on the arrival and persistence of another species can be characterized through analyses of sequential, paired observations of both species on focal habitat patches.

In addition to distinguishing the multiple mechanisms structuring communities, temporal patterns can be used to characterize community turnover through time. Temporal turnover (i.e., compositional changes in a single patch through time) can be compared to spatial turnover (i.e., compositional changes between patches across space) as a measure of compositional consistency through time (Anderson et al. 2011). Within-patch turnover rates can also be considered for individual species as a metric of site-attachment relative to focal habitat patches. While most species that are spatially rare are expected to be transient in the focal community (and perhaps

common in a different community; Sgarbi and Melo 2017), some uncommon species may be persistent on habitat patches through time. Persistence of rare species may be due to (1) strong associations with the patch due to patch-specific habitat characteristics or (2) strong site-attachment regardless of patch quality (e.g., sessile benthic organisms). Transient behavior is expected for species that use a patch as temporary habitat, but can also be observed for species that have a home range that expands over multiple patches. Temporal surveys can complement spatial surveys by helping to distinguish species that are spatially rare in communities due to transient associations with focal habitat patches from species that are spatially rare despite temporal persistence on habitat patches.

Here, we compare spatial and temporal variation in the composition of communities associated with the branching coral, *Pocillopora meandrina*. In this system, *P. meandrina* is a structure-forming foundation species that creates spatially discrete habitat patches that are utilized by communities of reef fishes and invertebrates. We tracked focal colonies by surveying their associated communities at monthly intervals for 3.5 years at two sites with distinct environmental conditions. Using this spatiotemporal dataset, we tested whether the rate of temporal, within-colony community divergence was consistent between colonies and sites, and whether there was convergence between spatial and temporal community turnover. We also compared species-specific within-colony turnover, expecting that differences in persistence would be related to each species' relationships with the host colony; i.e., strong interactors (mutualists, parasites) would be more consistent through time than species with more diffuse interactions (commensals, facultative species). Next, we tested whether the spatiotemporal differences in colony-scale community composition were more closely related to colony characteristics or regional biophysical drivers. We also tested the influence of temporal fluctuations in biophysical drivers on site-scale patterns in community composition and diversity metrics. Finally, we evaluated potential species interactions by quantifying arrival and persistence probabilities within two taxonomic groups, i.e., trapeziid crabs and Scorpaenidae fishes, that have been shown to have non-random spatial co-occurrence patterns (Counsell et al. 2018). Overall, this study characterizes temporal patterns in coral-associated communities at both patch and metacommunity scales, and emphasizes potential mechanisms driving variation in these communities.

Methods

Survey Sites

From spatial surveys of *Pocillopora*-associated communities around the island of O'ahu (Counsell et al. 2018), two sites were identified for repeated surveys over time based on the abundance of available focal colonies and the relative ease of access for repetitive sampling. The first site is on the south shore of O'ahu near the University of Hawai'i Kewalo Marine Laboratory and was accessed from shore (21.2898°N, -157.8628°W); the second site is located in Kāne'ohe Bay on the windward side of O'ahu and was accessed via small boat from the Hawai'i Institute of Marine Biology (21.4564°N, -157.7945°W). *Pocillopora meandrina* at these sites host coral-associated communities that are similar to those found at other forereef and sheltered sites around O'ahu (Counsell et al. 2018). The Kewalo site included 22 colonies ranging in depth from 7.0 to 8.6 m (mean = 7.7 m); the Kāne'ohe Bay site included 20 colonies ranging in depth from 2.6 to 3.6 m (mean = 3.2 m).

Community Surveys

The fish and invertebrate communities associated with focal *P. meandrina* were repeatedly surveyed on SCUBA for more than three years (June 2014 to November 2017). One diver (author CWWC) consistently surveyed the cryptic communities, and another diver photographed host colonies and the immediately adjacent benthic habitat (for additional details see Chapter Two). Surveys were conducted monthly with 33±8 days (mean±SD) between surveys, although logistical constraints stretched the range of survey intervals from 22 to 71 days. For two months in 2014 (June and July) and one month in 2017 (May), surveys were conducted weekly with 7±1 days (mean±SD) between surveys. In total, the colonies at Kewalo were surveyed 50 times, and the colonies at Kāne'ohe Bay were surveyed 48 times, resulting in 1,437 surveys of coral-associated communities.

Surveys targeted individuals >5 mm. At this size, trapeziid crabs were consistently identifiable to the species level. Hermit crabs of the Paguroidea superfamily, sea slugs of the Chromodorididae family, mantis shrimp, *Drupella* snails, and vermetid snails could not be consistently identified to species and were grouped at these higher taxonomic levels. In addition, "*Sebastapistes* complex" was used for a set of three visually similar scorpionfish species (*S.*

fowleri, *S. galactacma*, and *S. ballieui*); "*Saron* spp." is used to group two cleaner shrimps (*S. marmoratus* and *S. neglectus*). Despite these limitations, a previous study that used a similar technique confirmed that visual surveys were 97% accurate in identifying species and estimating abundance of the cryptofaunal community (Sin and Lee 2000).

Colony Characteristics

Genetic tests were used to confirm the species identity of host colonies as *P. meandrina* (Johnston et al. 2018). Depth at the colony base, inter-branch distance, and colony size were measured once for each colony (Table 3.1). In addition, colony-scale percent live coral tissue and percent bleached were estimated at each time step. Over the course of the time series, some colonies showed significant declines in health. To maintain comparisons between similar quality habitat patches, colonies that maintained a percent live estimate between 80 and 100% were retained throughout the full time series, while colonies that dropped below 75% live were removed from the time series at the point that their live tissue estimate dropped below 90%.

Community Turnover

To examine community turnover through time, the Jaccard dissimilarity was calculated between a colony and itself for all pairs of time steps for the 36 colonies that were followed for at least one year. This amounted to 27,820 within-colony temporal community comparisons along a temporal gradient ranging from 5 to 1,264 days between surveys. There were two goals of this analysis: (1) to compare the dynamics of within-colony community turnover through time with colony-scale characteristics, and (2) to test whether temporal dissimilarity (i.e., community distance between a colony at time *t* and the same colony at some future time) converges with spatial dissimilarity (i.e., community distance between two different colonies at the same time). Jaccard dissimilarity was modeled as a saturating function of the time between community surveys such that $dissimilarity\ (\Delta t) = \Phi_1 + (\Phi_2 - \Phi_1) \times e^{-\Phi_3 \times \Delta t}$, where Φ_1 is the asymptote, Φ_2 is the y intercept, and Φ_3 is the growth parameter. Using AIC scores, we compared models where Φ_1, Φ_2, or Φ_3 were shared between colonies, i.e., we tested the hypotheses that (i) all colonies converge to the same degree of dissimilarity as temporal distance increases (shared Φ_1), (ii) all colonies diverge similarly in the first time step (shared Φ_2), or (iii) all colonies turnover at the same rate (shared Φ_3). We also ran a set of models for which the

intercept, Φ_2, was set to zero such that $dissimilarity\ (\Delta t) = \Phi_1(1 - e^{-\Phi_3 \times \Delta t})$. For the best model, we tested whether the best linear unbiased predictors (BLUPs) for the parameter(s) that varied across coral colonies were a function of colony characteristics (Table 3.1). To test whether temporal dissimilarity converges to spatial dissimilarity, we calculated spatial dissimilarity as the temporal mean of the average between colony Jaccard dissimilarity based on nine randomly selected colonies from each time step. Colonies were randomly selected at each time step to minimize autocorrelation between spatial dissimilarity estimates at sequential time steps; nine was the lowest number of healthy colonies surveyed within a given time step.

We characterized the rate of persistence for each species as the proportion of times that the species was present at time $t+1$, given that it was there at time t, across all corals. This persistence rate was compared to the mean spatial occupancy, i.e., proportion of corals occupied by that species averaged across all time steps. The observed data were compared to a null model of persistence in which species have consistent mean spatial occupancies, but no association with individual habitat patches. The persistence null model (mean±95% CI) was calculated from 1,000 simulations of species with mean spatial occupancies varying from 0.01 to 1 of 50 habitat patches considered over 50 time steps. A generalized linear mixed model was used to describe the observed relationship between persistence and mean spatial occupancy across all species. The model included a random effect of species relation to host colony (i.e., mutualist known to benefit the coral, parasite known to harm the coral, or commensal with no known effect on the coral; Tables 3.S1 & 3.S2) and had a binomial error distribution. An additional generalized linear model was run to determine whether the deviation between a species' observed persistence and their persistence predicted by the null model (i.e., their mean spatial occupancy) was different between species known to have strong interactions with the host coral (i.e., mutualists and parasites) and commensal species.

Biophysical Drivers

To identify drivers of temporal dynamics in community structure, we tested how community composition, patch occupancy, alpha diversity, and beta diversity varied as functions of colony characteristics and biophysical parameters (Table 3.1). Three biophysical parameters previously identified as major drivers of coral reef ecosystem state (Gove et al. 2013) were

considered: chlorophyll-a (proxy for phytoplankton biomass), wave height (measure of underwater disturbance), and sea surface temperature (affects various ecological processes, follows seasonal and inter-annual forcing). Daily data for surface chlorophyll-a concentration at both survey sites were accessed from the National Oceanic and Atmospheric Administration's (NOAA) National Polar-orbiting Partnership satellite's Visible Infrared Imaging Radiometer Suite (VIIRS) through NOAA CoastWatch's ERDDAP for the noaa_nesdis_9050_80f5_7292 dataset. Estimates of chlorophyll-a concentration from satellite data are sensitive to cloud coverage, and as a result, this dataset had a large number of missing values. To describe general temporal shifts in productivity and to effectively handle the missing data, surface chlorophyll-a concentration was calculated as the monthly mean of all available data within the 29 days prior to and including each survey date. Hourly significant wave height data were accessed from the Pacific Islands Ocean Observing System's (PacIOOS) Simulating WAves Nearshore (SWAN) Regional Wave Model through PacIOOS's ERDDAP for the SWAN_Oahu_Best dataset. For each survey date, the daily maximum significant wave height value was used to depict variation in water flow disturbance levels. One survey time at each site occurred during a window when wave height data were missing; for these two data points the maximum value from the closest day with data was used (seven days prior to the survey date for both). Daily sea surface temperature (SST) data were accessed from the Group for High Resolution Sea Surface Temperature via the University of Hawai'i's School of Ocean and Earth Science and Technology through NOAA's ERDDAP for the hawaii_soest_1923_466e_2627 dataset. These data were summarized as weekly means using data for the six days prior to and including each survey date.

Partial Mantel tests were used to evaluate whether temporal variability in community composition (Bray-Curtis distance) at the colony-scale was related to (i) colony characteristics, (ii) biophysical parameters, or (iii) both colony characteristics and biophysical parameters (Table 3.1), conditional on temporal distance. Each set of environmental variables and temporal distance were represented as matrices of Euclidean distances. We also tested a model of species occupancy through time at the site-scale, relating species-specific patch occupancy (Bray-Curtis community distance matrix based on proportion of colonies occupied by a species at each time step) to the biophysical distance matrix conditional on the temporal distance matrix.

Generalized linear models were used to test for effects of individual biophysical drivers on alpha and beta diversity; these diversity parameters were detrended prior to analyses (i.e., response variable for each model was the residuals from a linear model of the diversity parameter as a function of time). At the colony-scale, we used a linear mixed model of alpha diversity (species richness) with colony characteristics and biophysical parameters (Table 3.1) as fixed effects, and survey date and colony identifier as random effects. At the site-scale, we tested how alpha diversity (mean species richness among colonies at each time) and beta diversity (mean Jaccard dissimilarity distance between all colony pairs at each time) varied with biophysical parameters through time. In all cases, colony characteristics and biophysical parameters were centered and scaled, and communities from the two sites were analyzed separately.

Species Transition Probabilities

To investigate how the presence of a species affects the arrival and persistence of other species, species-specific transition probability models were developed using generalized linear mixed models (GLMMs) with coral colony nested in site as random effects and binomial error distributions. We focused on two families highlighted in spatial surveys as having a large number of non-random co-occurrences (Counsell et al. 2018): the Trapeziidae crabs (five species) and the Scorpaenidae fishes (three species). To test whether the arrival probability of each focal species was influenced by the presence of other species in the community, the data were subset to time steps in which the focal species was not present at time *t* and then GLMMs were used to test whether the probability of arrival (presence) or non-arrival (absence) at time *t+1* was explained by the presence or absence of other species within the same family at time *t*. For persistence probability models, the data were subset to include only time steps for which the focal species was present at time *t*; the GLMMs modeled the persistence (presence) or departure (absence) of the focal species at time *t+1* as a function of the presence or absence of other species within the same family at time *t*.

All statistical analyses in this chapter were conducted and coded in R (v 3.3.2) (R Development Core Team 2016) using packages: *car* (Fox and Weisberg 2011), *corrplot* (Wei and Simko 2017), *lme4* (Bates et al. 2015), *MuMIn* (Bartoń 2016), *nlme* (Pinheiro et al. 2016), *reshape2* (Wickham 2007), and *vegan* (Oksanen et al. 2017).

Results

Community Turnover

The best model of within-colony community dissimilarity over time held the rate of change in community dissimilarity constant across all colonies (Φ_3=0.002), but allowed variation across colonies nested in sites for the asymptotic temporal community dissimilarity (mean Φ_1=0.571) and the community dissimilarity at time steps approaching zero (mean Φ_2=0.296) (Table 3.S3, Fig. 3.1). Variance in both the asymptotic community dissimilarity ($\sigma_{\Phi_{1,site}}$=0.026, $\sigma_{\Phi_{1,colony}}$=0.163) and the community dissimilarity at time steps approaching zero ($\sigma_{\Phi_{2,site}}$<0.001, $\sigma_{\Phi_{2,colony}}$=0.073) was higher among colonies than between sites. There was no relationship between the colony-specific estimates of Φ_1 and Φ_2, and colony characteristics (Table 3.1) or maximum temporal distance (number of days between the first and last survey for each colony) (Fig. 3.S1). Temporal community dissimilarity did not converge with mean spatial dissimilarity at either site (Fig. 3.1): the site-level estimates of the temporal community dissimilarity asymptote ($\Phi_{1,Kāne'oheBay}$=0.556; $\Phi_{1,Kewalo}$=0.587) were lower than the average site-level spatial community dissimilarities (Kāne'ohe Bay=0.624, 0.605 to 0.642 95% CI; Kewalo=0.607, 0.593 to 0.621 95% CI).

The model that allowed the rate of change in community dissimilarity (mean Φ_3=0.001) and the community dissimilarity at time steps approaching zero (mean Φ_2=0.306) to vary across colonies, while keeping the asymptote constant (Φ_1=0.718), had a similar fit to the previously described best model (ΔAIC=1.7, Table 3.S3); the results of this alternate model are presented in Figure 3.S2. While an intercept of zero would be logical given no change expected in a community surveyed repeatedly with zero time between surveys, the minimum amount of time between surveys in the dataset was five days, and models with the intercept set to zero had much worse model fit than the best model which included a non-zero intercept (ΔAIC >2,950; Table 3.S3).

Regarding the consistency of individual species on focal colonies through time, the null model depicted a 1:1 relationship between expected persistence and spatial occupancy for species simulated to have no site attachment, i.e., randomly distributed across colonies at each time step (Fig. 3.2). Of the 61 species observed in association with *P. meandrina* colonies over

the course of this study, 34 species persisted on colonies at a rate higher than predicted by the null model (Tables 3.S1 & 3.S2, Fig. 3.2). This included six known invertebrate mutualist species, one fish mutualist species, and two parasitic invertebrates, as well as 25 species with unknown effects on the host coral (Fig. 3.2). The persistence of a species on a colony was an increasing function of species average spatial occupancy (binomial GLMM $r^2_{marginal}$=0.921; Fig. 3.2); species' relationship with the host colony described no additional variance ($r^2_{conditional}$=0.921). However, species' relationship with the host colony did effect how different their observed persistence was from their expected persistence (i.e., their mean spatial occupancy) with mutualist and parasite species having an average deviation between observed and expected almost twice as large as that of commensal species (mean deviations of 0.386 and 0.205, respectively; p=0.027).

Environmental Drivers of Change in Community Composition

Colony-scale differences in community composition through space and time were associated more strongly with colony characteristics ($R^2_{Kāne'ohe\ Bay}$=0.145, R^2_{Kewalo}=0.240), than biophysical parameters ($R^2_{Kāne'ohe\ Bay}$=0.040, R^2_{Kewalo}=0.013) (Table 3.2). Site-scale variation in community composition through time, as measured by the proportional patch occupancy of each species, was not related to biophysical parameters (Table 3.2).

Mean community values for alpha and beta diversity (i.e., colony-scale species richness and Jaccard dissimilarity distances between colony pairs) showed site-specific temporal variation (Fig. 3.3d & 3.3e). Species richness increased with colony size at both sites, decreased with percent live coral tissue at Kewalo, and decreased with colony depth at the Kāne'ohe Bay site; no biophysical parameters contributed to species richness at the colony-scale (Table 3.3). At both sites, variation in species richness (after accounting for associations with colony characteristics and biophysical parameters) was higher among individual colonies than over survey dates (Kāne'ohe Bay $\sigma_{coral\ identity}$=0.043, $\sigma_{survey\ date}$=0.001; Kewalo $\sigma_{coral\ identity}$=0.015, $\sigma_{survey\ date}$=0.005) (Table 3.3). For diversity parameters at the site-scale, mean species richness increased with increasing significant wave height at Kewalo, and mean community dissimilarity decreased with increasing SST at Kāne'ohe Bay (Table 3.3).

Species Transition Probabilities

Of twenty possible trapeziid-trapeziid effects on arrival, there were two significant negative effects and four significant positive effects (Table 3.4): the presence of *T. intermedia* decreased the probability of arrival for *T. tigrina*, and *T. bidentata* decreased the probability of arrival for *T. intermedia*, while the presence of *T. digitalis* increased the probability of arrival for *T. intermedia*, *T. bidentata*, and *T. flavopunctata*, and *T. flavopunctata* increased the probability of arrival for *T. bidentata*. *T. tigrina* was the only species with no effect on the arrival of another trapeziid, and *T. digitalis* was the only trapeziid whose probability of arrival was not affected by the presence of other trapeziid species.

Of twenty possible trapeziid-trapeziid effects on persistence, there were four negative effects and two positive effects (Table 3.4). *T. intermedia* decreased the probability of persistence for *T. tigrina*, who, reciprocally, decreased the probability of persistence for *T. intermedia*. In addition, *T. flavopunctata* decreased the probability of persistence for *T. intermedia*, and *T. bidentata* decreased the probability of persistence for *T. tigrina*. *T. digitalis* increased the probability of persistence for *T. intermedia*, and *T. flavopunctata* increased the probability of persistence for *T. digitalis*.

Across the three species of Scorpaenidae, there was one positive effect on the probability of arrival and one negative effect on the probability of persistence (Table 3.5). *C. typicus* increased the probability of arrival for *S. coniorta*. The *Sebastapistes* complex decreased the probability of persistence for *C. typicus*.

Discussion

Communities associated with *P. meandrina* habitat patches showed strong evidence of niche-based processes. Within-colony community dissimilarity increased through time, but never reached average between colony community dissimilarity (Fig. 3.1). This indicates that habitat characteristics of individual colonies filter communities (i.e., species sorting), such that communities remain fundamentally more similar on the same colony through time than across nearby colonies at the same time. Species sorting processes were further supported by the consistency in community composition observed through patterns of species-specific turnover on colonies through time (Fig. 3.2). Thirty-four of sixty-one species, including species that occurred

on less than 10% of colonies spatially, were observed to persist on their host colony more often than expected given a null model based on spatial occupancy rates. This type of non-random patch habitat association follows the expectations for species that have arrived at a habitat patch that optimizes their fitness (i.e., environmental filtering) and/or have low emigration rates (Leibold 2009).

Coral-associated communities did not show strong responses to temporal variation in biophysical drivers, i.e., daily maximum significant wave height, weekly mean sea surface temperature (SST), and monthly mean surface chlorophyll-a concentration (Tables 3.2 & 3.3, Fig. 3.3). Spatiotemporal variation in community composition was significantly, but weakly, associated with biophysical parameters and was more strongly associated with colony characteristics (Table 3.2). At the site-scale, biophysical drivers showed no relationship with proportional patch occupancy of species through time. Further, species richness and community dissimilarity showed no consistent association with biophysical drivers through time (Table 3.3). Wave height was positively associated with mean species richness at Kewalo, suggesting that additional species utilize the sheltered habitat of the coral branches in higher wave energy conditions (Table 3.3). This same pattern of increased species richness with increased wave energy was also noted for *Pocillopora* associated communities over spatial gradients (Counsell et al. 2018), suggesting that this biophysical parameter may affect community formation and maintenance processes. The lower overall wave energy and limited range of wave energy at the Kāneʻohe Bay site (Fig. 3.3b) may explain why this driver was only correlated with diversity metrics for Kewalo communities.

Pocillopora associated communities have lower abundances and species richness with increasing chlorophyll-a over spatial gradients (Counsell et al. 2018), and some trapeziid species have decreased colony-scale abundances in response to experimentally increased water temperatures (Stella et al. 2011a, 2014). However, these biophysical drivers were not strongly associated with temporal variation in communities in this study. Support for spatial, but not temporal association with chlorophyll-a suggests that this driver may structure community formation processes by affecting connectivity and species arrival to sites, but does not affect ongoing community maintenance processes. SST was negatively associated with mean community dissimilarity at Kāneʻohe Bay, suggesting some species are responding to temporal

shifts in water temperature. Not finding a consistent association between community metrics and temporal shifts in SST suggests that the range of SST observed may not have created a strong enough gradient of thermal stress. The effect of environmental filtering on community composition can strengthen as stress increases (Li and Shipley 2018). There could also be a temporal mismatch between the SST metric used and the community's response to changes in SST. Changes in community composition associated with shifting environmental conditions can exhibit a temporal lag (Graham et al. 2007).

In contrast to the minimal effects of biophysical parameters on coral-associated communities, our results supported the importance of species sorting dynamics relative to patch habitat quality parameters for temporal patterns in coral-associated communities. The temporal dynamics of within-colony community dissimilarity suggested higher variation among colonies than between sites (Fig. 3.1). Similarly, species richness had an order of magnitude more variance associated with colony identity than with survey date (Table 3.3), even after accounting for variance explained by colony characteristics included in the model (Table 3.1). This analysis reinforced a commonly observed positive association between habitat patch size and species richness (Arrhenius 1921; Abele and Patton 1976; Counsell et al. 2018), as well as a negative association between species richness and percent live coral tissue at Kewalo and a negative association between species richness and depth at Kāne'ohe Bay (Table 3.3). These results support species sorting dynamics relative to the quality of the patch habitat with differences in colony characteristics accounting for 15% of the variation in community composition at Kewalo and 24% at Kāne'ohe Bay (Table 3.2).

The species sorting metacommunity paradigm poses that species select patches to optimize fitness across abiotic and biotic patch habitat conditions (Leibold et al. 2004). Our results showed that species interactions influenced community composition at the habitat patch scale through within taxa effects on species arrival to and persistence on colonies. Transition probability models showed significant effects for particular species pairs within taxonomic groups, reinforcing evidence of strong interactions within these species complexes that were previously highlighted with a co-occurrence model (Counsell et al. 2018, relevent details reprinted in Tables 3.4 & 3.5). The positive association between the presence of *T. digitalis* and the arrival of three other trapeziid species as well as a positive association between *T. digitalis*

and the persistence of *T. intermedia* strongly suggests that *T. digitalis* facilitates the colonization of other trapeziid species (Table 3.4). These positive associations between *T. digitalis* and three of four other trapeziid species, combined with the observation that *T. digitalis* was the only trapeziid whose arrival was not affected by other trapeziids suggests that *T. digitalis* may be an early colonizer of patch habitats. Our results also suggest particularly high competition between *T. intermedia* and *T. tigrina* with both species decreasing the probability of persistence for the other species. Further, the negative association of *T. intermedia* with the probability of arrival for *T. tigrina* suggests that order of arrival may be important for these two species. Previous studies have suggested synergistic dynamics between trapeziid species with different species providing distinct protective benefits for host corals (McKeon et al. 2012; McKeon and Moore 2014). The facilitative patch dynamics observed in the current study for some species-species interactions further illuminates potential complementary components of the niches occupied by some trapeziid species.

Within the Scorpaenidae complex, *C. typicus* was positively associated with the arrival of *S. coniorta* suggesting that it facilitates colonization by *S. coniorta* (Table 3.5). However, the probability of *C. typicus* remaining on a colony is decreased in the presence of the *Sebastapistes* complex, suggesting that *C. typicus* is not a strong competitor for habitat patches. While evidence of competition and facilitation from studies of temporal dynamics is stronger than spatial co-occurrence data, it must still be interpreted cautiously. The patterns expected for various types of community dynamics may not be observed in communities that are exhibiting nonequilibrium dynamics (Loreau 2000; Hixon 2011). In addition, multiple underlying processes can interact resulting in community composition patterns that do not reflect a linear combination of the underlying processes (Hixon and Carr 1997; Barner et al. 2018). However, unlike spatial co-occurrence patterns, temporal patterns provide directionality of effects and enable separate models of arrival and persistence to further characterize potential competition-colonization tradeoffs that merit further experimental research.

Our results emphasize the importance of niche-based processes at the colony-scale in structuring tropical coral-associated communities through time. Species-sorting processes through both environmental filtering based on patch habitat quality and species interactions at the patch scale were emphasized. This research also identified a variety of species that were

more persistence on colonies than expected given their spatial occupancy, and therefore, these species are of particular interest for future studies into potential species interactions with the host colony. In addition, this research established a baseline measure of temporal variation for coral-associated cryptofaunal communities, data that are critical as coral reefs ecosystems face increased environmental stress and disturbance (Smith and Buddmeier 1992; Bellwood et al. 2004). This research elucidated important community dynamics that cannot be disentangled with spatial surveys and provided a template for temporal community analyses in other systems.

Table 3.1. Environmental driver variables, including the source of data, description of metric included in analyses, and type of parameter. Daily sea surface temperature data were accessed from the Group for High Resolution Sea Surface Temperature via the University of Hawai‘i’s School of Ocean and Earth Science and Technology through http://apdrc.soest.hawaii.edu/erddap/griddap/hawaii_soest_1923_466e_2627.html. Hourly significant wave height data were accessed from Pacific Islands Ocean Observing System’s Simulating WAves Nearshore Regional Wave Model through http://oos.soest.hawaii.edu/erddap/griddap/SWAN_Oahu_Best.html. Chlorophyll-a concentration data for both survey sites were accessed from NOAA’s National Polar-orbiting Partnership satellite’s Visible Infrared Imaging Radiometer Suite (VIIRS) daily dataset through https://oceanwatch.pifsc.noaa.gov/erddap/griddap/noaa_nesdis_9050_80f5_7292.html.

Parameter Type	**Parameter (units)**	**Measurement**	**Data Source**
Biophysical parameters (temporally dynamic)	sea surface temperature (°C)	weekly mean (6 days prior to and including survey date)	Dataset ID: hawaii_soest_1923_466e_2627
	significant wave height (m)	maximum value for survey date	Dataset ID: SWAN_Oahu _Best
	surface chlorophyll-a concentration (mg^{-m3})	monthly mean (29 days prior to and including survey date)	Dataset ID: noaa_nesdis_9050_80f5_7292
Colony characteristics (temporally static)	colony size (cm)	$(length \times width \times height)^{1/3}$	*in situ* measurements
	inter-branch distance (cm)	mean of five measurements	*in situ* measurements
	depth (m)	base of colony	*in situ* measurements
Colony characteristics (temporally dynamic)	percent live coral tissue (%)	visual estimate	*in situ* estimates confirmed with photo references
	percent bleached (%)	visual estimate	*in situ* estimates confirmed with photo references

Table 3.2. Partial Mantel statistic R^2s are presented for a set of tests run with Bray-Curtis community based distances as the response matrix and an environmental matrix of colony characteristics, biophysical parameters, or both (Table 3.1) as the explanatory matrix. All comparisons were conditional on temporal distance. For both sites, most variation in community composition was explained by colony characteristics. Mantel statistics that are significant at $p < 0.05$ are in listed in bold.

Community Matrix	Environmental Matrix	Kāne‘ohe Bay (R^2)	Kewalo (R^2)
Colony-scale species abundance	Colony characteristics	**0.145**	**0.240**
	Biophysical parameters	**0.040**	**0.013**
	Colony characteristics + biophysical parameters	**0.126**	**0.200**
Site-scale species occupancy	Biophysical parameters	0.085	0.096

Table 3.3. Effect sizes (parameter estimates) for biophysical parameter and colony characteristic predictor variables (Table 3.1) from regression models on community level diversity metrics (bold if significant at $p < 0.05$). Prior to analyses all predictor variables were centered and scaled, and response variables were detrended through time. R^2 values are marginal, i.e., only based on the fixed effects, for the models that included random effect intercepts (REs) for survey date and individual coral colonies. R^2 values for the other models with mean metrics as the response variable correspond to the adjusted R^2.

Site	Response variable	Biophysical parameters			Colony characteristics				R^2	Variance for REs
		SST	Wave	Chl-a	Size	Depth	% live coral tissue	% bleached		
Kāneʻohe Bay	Species richness	0.020	-0.009	<0.001	**0.228**	**-0.116**	-0.012	-0.004	0.303	date: 0.001 coral: 0.043
	Mean species richness	0.064	-0.056	-0.010					0.010	
	Mean community dissimilarity	**-0.016**	-0.001	0.003					0.056	
Kewalo	Species richness	0.015	0.016	0.026	**0.219**	-0.003	**-0.059**	<0.001	0.556	date: 0.005 coral: 0.015
	Mean species richness	0.083	**0.220**	0.008					0.072	
	Mean community dissimilarity	0.007	-0.006	0.009					0.028	

Table 3.4. Effect sizes (parameter estimates) for the presence of taxonomically similar species at time *t* on the probability of arrival (top) or persistence (middle) for each of five trapeziid species at time *t+1* from generalized linear mixed models. Effect sizes significant at p <0.1 are colored red for negative effects and blue for positive effects. Effect sizes significant at p <0.05 are in bold. The bottom table displays non-random spatial co-occurrences (negative in red, positive in blue; spatial co-occurrence between $species_a$ and $species_b$ is the same as between $species_b$ and $species_a$) from a survey of 751 colonies across 19 different sites (Counsell et al. 2018).

		Effect of species presence at time *t*				
		T. intermedia	*T. tigrina*	*T. digitalis*	*T. flavopunctata*	*T. bidentata*
Arrival at time *t+1* (n = times absent at time *t*)	*T. intermedia* (n=517)		-0.271	**1.195**	-0.518	**-2.091**
	T. tigrina (n=718)	**-2.055**		-0.627	0.298	-0.426
	T. digitalis (n=855)	-0.616	-0.476		0.937	-1.299
	T. flavopunctata (n=1222)	0.421	0.791	**1.395**		0.133
	T. bidentata (n=1302)	0.381	0.352	**1.387**	**1.652**	
Persistence at time *t+1* (n = times present at time *t*)	*T. intermedia* (n=878)		**-1.905**	**1.092**	**-1.737**	-0.014
	T. tigrina (n=677)	**-1.014**		-0.621	-0.760	**-1.231**
	T. digitalis (n=540)	0.315	-0.187		**1.711**	-0.198
	T. flavopunctata (n=173)	0.379	-0.799	0.992		20.554
	T. bidentata (n=93)	-0.293	-1.219	0.161	-0.216	
Non-random spatial co-occurrence	*T. intermedia*					
	T. tigrina					
	T. digitalis					
	T. flavopunctata					
	T. bidentata					

Table 3.5. Effect sizes (parameter estimates) for the presence of taxonomically similar species at time *t* on the probability of arrival (top) or persistence (middle) for each of three Scorpaenidae species at time *t+1* from generalized linear mixed models. Effect sizes significant at p <0.1 are colored red for negative effects and blue for positive effects. Effect sizes significant at p <0.05 are in bold. *S.* complex refers to a species complex of three visually similar scorpionfish species (*Sebastapistes fowleri*, *S. galactacma*, and *S. ballieui*) that were not consistently distinguished to species. The bottom table displays non-random spatial co-occurrences (negative in red, positive in blue; spatial co-occurrence between $species_a$ and $species_b$ is the same as between $species_b$ and $species_a$) from a survey of 751 colonies across 19 different sites (Counsell et al. 2018).

		Effect of species presence at time *t*		
		C. typicus	*S. coniorta*	*S.* complex
Arrival at time *t+1* (n = times absent at time *t*)	*C. typicus* (n=1151)		-2.239	1.297
	S. coniorta (n=976)	**1.385**		0.731
	S. complex (n=826)	-0.985	-0.231	
Persistence at time *t+1* (n = times present at time *t*)	*C. typicus* (n=244)		0.216	**-2.690**
	S. coniorta (n=419)	-0.590		-0.647
	S. complex (n=569)	0.921	-0.638	
Non-random spatial co-occurrence	*C. typicus*			
	S. coniorta			
	S. complex			

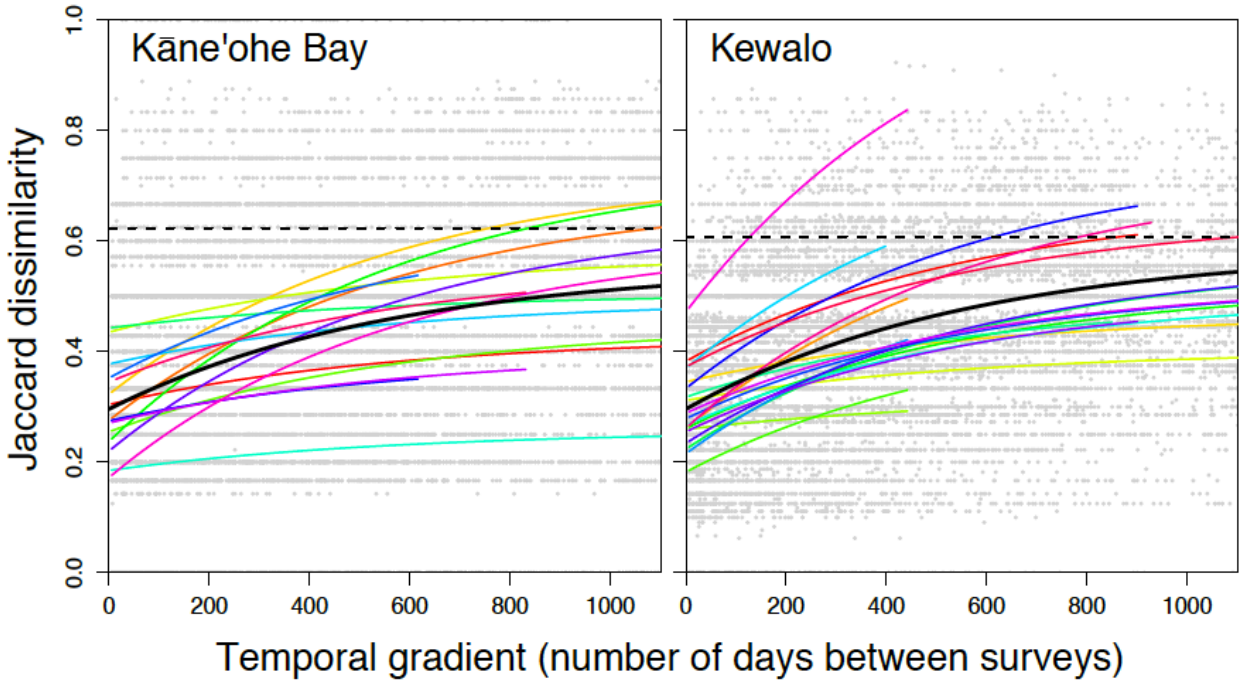

Figure 3.1. Within-colony community dissimilarity (gray dots) across a temporal gradient is shown separately for communities at two survey sites. A non-linear model was used to estimate the rate of change, the intercept, and the asymptote for this relationship while allowing variation in the intercept and asymptote across individual colonies nested in sites. The mean site-scale patterns are shown with a solid black line, and colony-scale trends are shown with multi-colored lines for colony-specific ranges along the temporal gradient. The average between colony spatial community dissimilarity for each site is shown with a black dashed line.

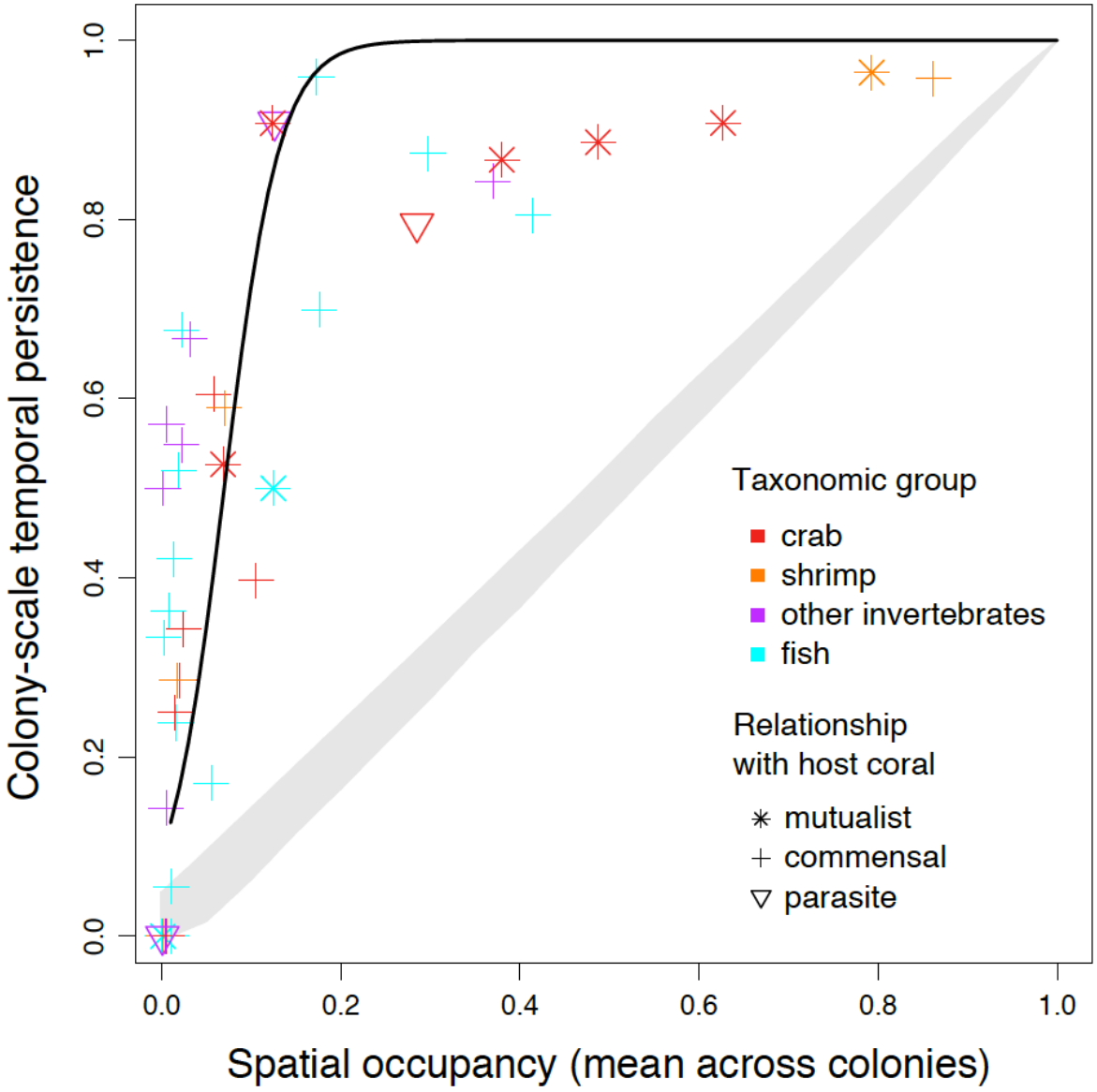

Figure 3.2. For each of 61 observed species (Tables 3.S1 & 3.S2), the probability of occurrence on colonies was averaged across surveys (mean spatial occupancy across colonies) and compared to the proportion of times the species was observed on an individual colony both at time *t* and at time *t+1* (colony-scale persistence through time). The species data are colored by taxonomic groups (i.e., crab, shrimp, other invertebrate, or fish) and shaped based on their relationship with the host coral (i.e., known mutualist, known parasite, or commensal with unknown effects on host coral). The relationship between spatial occupancy and temporal persistence was modeled with a generalized linear mixed model (black line). A community simulation depicts the expected relationship between spatial occupancy and temporal persistence given random distributions across colonies at each time step (gray line represents 95% confidence intervals based on 1000 simulations for sets of 21 distinct spatial occupancy probabilities across 50 colonies over 50 time steps).

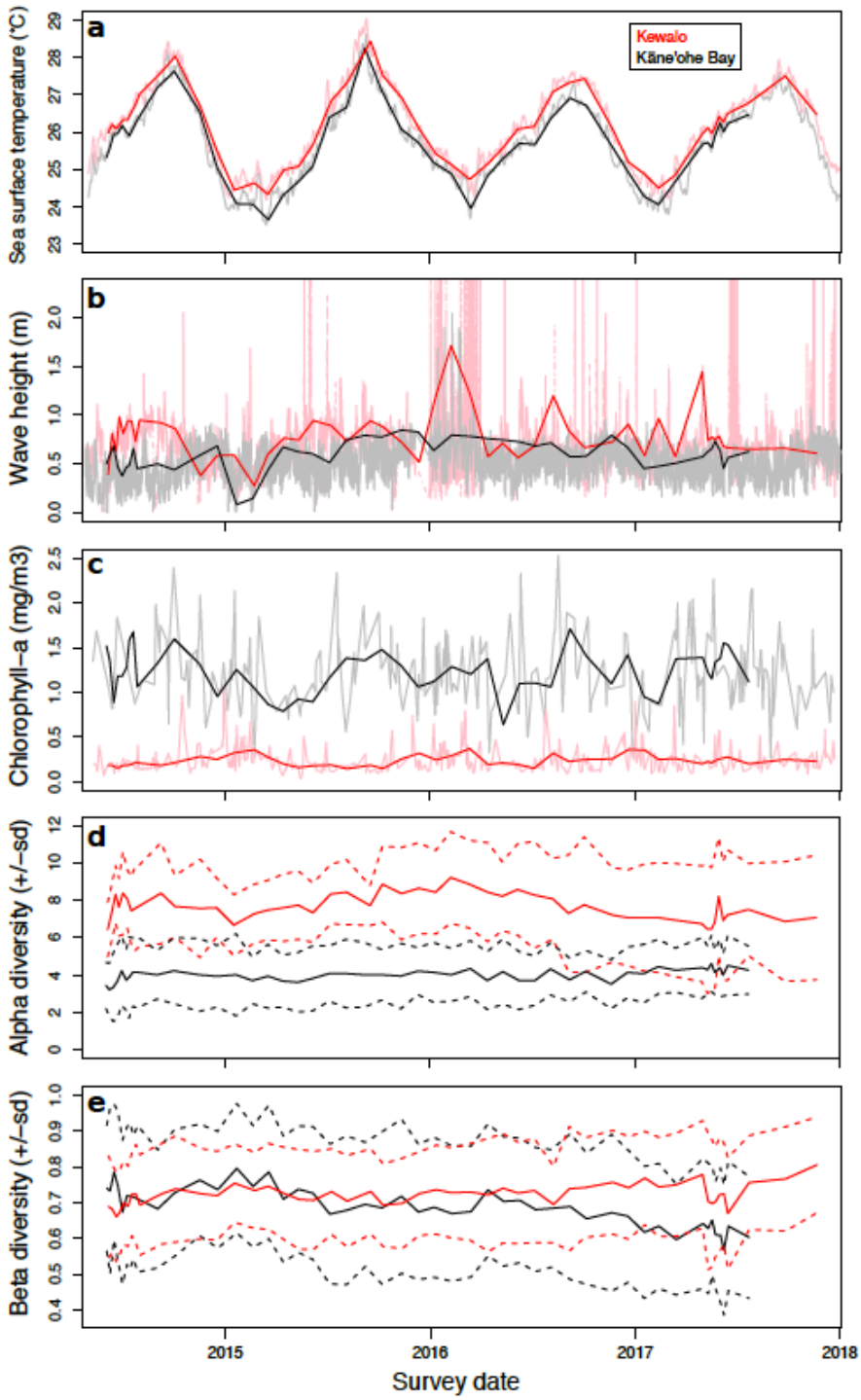

Figure 3.3. Original data (Table 3.1) for sea surface temperature (a), significant wave height (b), and surface chlorophyll-a concentration (c) presented in faded colors. Overlaid are summarized versions of these data relative to survey dates (weekly average, daily maximum, and monthly average, respectively). (d) Average alpha diversity, i.e., species richness, and (e) average beta diversity, i.e., Jaccard community dissimilarity distances (e), for each survey date. Data specific to Kewalo are in red, and data specific to Kāne‘ohe Bay are in black.

Table 3.S1. Family, genus, species, and relation to host coral based on literature (i.e., mutualist with known benefits, parasite with known negative effects, or commensal with unknown effects) for species observed during repeated surveys (>3 years) on focal colonies (n=42). Species are listed in descending order relative to their persistence on individual colonies (the probability that they were observed on the same colony for two consecutive time steps). Only includes the species that were more persistent than predicted for their observed spatial occupancy (proportion of colonies occupied, averaged across time steps) based on a null model with random distributions across colonies at each timestep (Fig. 3.2).

Family	**Genus**	**Species**	**Relation to host coral**	**Temporal persistence**	**Spatial occupancy**
Alpheidae	*Alpheus*	*lottini*	mutualist	0.964	0.793
Scorpaenidae	*Caracanthus*	*typicus*	commensal	0.959	0.173
Palaemonidae	*Harpiliopsis*	*depressa*	commensal	0.958	0.861
Muricidae	*Quoyula*	*monodonta*	parasite	0.909	0.126
Trapeziidae	*Trapezia*	*intermedia*	mutualist	0.908	0.627
Trapeziidae	*Trapezia*	*flavopunctata*	mutualist	0.908	0.124
Trapeziidae	*Trapezia*	*tigrina*	mutualist	0.886	0.487
Scorpaenidae	*Sebastapistes*	*coniorta*	commensal	0.874	0.297
Trapeziidae	*Trapezia*	*digitalis*	mutualist	0.867	0.380
Ophiocomidae	*Ophiocoma*	*pica*	commensal	0.843	0.370
Scorpaenidae	*Sebastapistes*	complex	commensal	0.805	0.414
Cryptochiridae	*Utinomiella*	*dimorpha*	parasite	0.795	0.285
Cirrhitidae	*Amblycirrhitus*	*bimacula*	commensal	0.699	0.176
Blenniidae	*Exallias*	*brevis*	commensal	0.676	0.022
Ophiocomidae	*Ophiocoma*	*erinaceus*	commensal	0.667	0.031
Xanthidae	*Pseudoliomera*	*speciosa*	commensal	0.605	0.058
Hippolytidae	*Saron*	spp.	commensal	0.589	0.070
Cypraeidae	*Cypraea*	*tigris*	commensal	0.571	0.005
Sabellidae	*Sabellastarte*	*spectabilis*	commensal	0.548	0.022
Trapeziidae	*Trapezia*	*bidentata*	mutualist	0.527	0.069
Cirrhitidae	*Paracirrhites*	*arcatus*	commensal	0.520	0.019
Pomacentridae	*Plectroglyphididon*	*johnstonianus*	mutualist	0.500	0.125
Aiptasiidae	*Aiptasia*	*pulchella*	commensal	0.500	0.001
Acanthuridae	*Acanthurus*	*nigrofuscus*	commensal	0.421	0.014
Paguroidea		spp.	commensal	0.397	0.105
Cirrhitidae	*Cirrhitops*	*fasciatus*	commensal	0.364	0.007
Xanthidae	*Domecia*	*hispida*	commensal	0.343	0.024
Acanthuridae	*Acanthurus*	*blochii*	commensal	0.333	0.002
Portunidae	*Charybdis*	*hawaiensis*	commensal	0.286	0.021
Palaemonidae	*Palaemon*	*pacificus*	commensal	0.286	0.017
Grapsidae	*Percnon*	*planissimum*	commensal	0.250	0.015
Tetraodontidae	*Canthigaster*	*jactator*	commensal	0.238	0.016
Labridae	*Thalassoma*	*duperrey*	commensal	0.171	0.055
Diadematidae	*Echinothrix*	*calamaris*	commensal	0.143	0.005

Table 3.S2. Family, genus, species, and relation to host coral based on literature (i.e., mutualist with known benefits, parasite with known negative effects, or commensal with unknown effects) for species observed during repeated surveys (>3 years) on focal colonies (n=42). Species are listed in descending order relative to their persistence on individual colonies (the probability that they were observed on the same colony for two consecutive time steps). Only includes the species whose persistence was similar to or less than that predicted for their observed spatial occupancy (proportion of colonies occupied, averaged across time steps) based on a null model with random distributions across colonies at each timestep (Fig. 3.2).

Family	**Genus**	**Species**	**Relation to host coral**	**Temporal persistence**	**Spatial occupancy**
Labridae	*Pseudocheilinus*	*tetrataenia*	commensal	0.056	0.011
Monacanthidae	*Cantherhines*	*verecundus*	commensal	0	0.001
Chaetodontidae	*Chaetodon*	*multicinctus*	commensal	0	0.001
Pomacentridae	*Dascyllus*	*albisella*	mutualist	0	0.002
Scorpaenidae	*Dendrochirus*	*barberi*	commensal	0	0.001
Muraenidae	*Echidna*	*polyzona*	commensal	0	0.001
Labridae	*Gomphosus*	*varius*	commensal	0	0.011
Muraenidae	*Gymnothorax*	*meleagris*	commensal	0	0.001
Ophichthidae	*Myrichthys*	*magnificus*	commensal	0	0.001
Cirrhitidae	*Paracirrhites*	*forsteri*	commensal	0	0.001
Monacanthidae	*Pervagor*	*aspricaudus*	commensal	0	0.001
Monacanthidae	*Pervagor*	*spilosoma*	commensal	0	0.001
Apogonidae	*Pristiapogon*	*kallopterus*	commensal	0	0.001
Labridae	*Pseudocheilinus*	*octotaenia*	commensal	0	0.001
Scaridae	*Scarus*	*psittacus*	commensal	0	0.002
Aethridae	*Actaeomorpha*	*erosa*	commensal	0	0.001
Carpiliidae	*Carpilius*	*convexus*	commensal	0	0.002
Chromodorididae		spp.	commensal	0	0.002
Diadematidae	*Echinothrix*	*diadema*	commensal	0	0.004
Xanthidae	*Etisus*	*demanipale*	commensal	0	0.002
Cidaridae	*Eucidaris*	*metularia*	commensal	0	0.002
Echinometridae	*Heterocentrotus*	*mamillatus*	commensal	0	0.001
Xanthidae	*Platypodia*	*eydouxii*	commensal	0	0.001
Portunidae	*Portunus*	*longispinosus*	commensal	0	0.001
Stomatopoda (Suborder)		spp.	commensal	0	0.002
Portunidae	*Thalamita*	*coerulipes*	commensal	0	0.006
Vermetidae		spp.	parasite	0	0.001

Table 3.S3. AIC scores from a set of models describing how within-colony community dissimilarity varies across a temporal gradient: $dissimilarity\ (\Delta t) = \Phi_1 + (\Phi_2 - \Phi_1) \times e^{-\Phi_3 \times \Delta t}$. In all models, Φ_1 is the asymptote of predicted maximum within-colony dissimilarity reached after long periods of time between surveys; Φ_2 is the intercept for within-colony dissimilarity predicted when there is no time between surveys; and Φ_3 is the rate of increase for within-colony dissimilarity as the amount of time between surveys increases. For each model, the parameters that were allowed to vary by coral colony nested in site are in bold. For some models, the intercept Φ_2 was set to zero: $dissimilarity\ (\Delta t) = \Phi_1 \times (1 - e^{-\Phi_3 \times \Delta t})$. Models were run with a maximum of 2,000 iterations, a maximum of 14 iterations for the penalized nonlinear least squares optimization step within the model optimization algorithm, and a minimum factor of 0.0000001 by which to shrink the default step size. Three models did not reach convergent solutions.

Model	Parameters that vary by coral nested in site	AIC	ΔAIC
$dissimilarity\ (\Delta t) = \Phi_1 + (\Phi_2 - \Phi_1) \times e^{-\Phi_3 \times \Delta t}$	--	-15581.07	5308.11
$dissimilarity\ (\Delta t) = \mathbf{\Phi_1} + (\Phi_2 - \mathbf{\Phi_1}) \times e^{-\Phi_3 \times \Delta t}$	Φ_1	-19988.65	900.53
$dissimilarity\ (\Delta t) = \Phi_1 + (\mathbf{\Phi_2} - \Phi_1) \times e^{-\Phi_3 \times \Delta t}$	Φ_2	-19725.73	1163.45
$dissimilarity\ (\Delta t) = \Phi_1 + (\Phi_2 - \Phi_1) \times e^{-\mathbf{\Phi_3} \times \Delta t}$	Φ_3	-20091.92	797.26
$dissimilarity\ (\Delta t) = \mathbf{\Phi_1} + (\mathbf{\Phi_2} - \mathbf{\Phi_1}) \times e^{-\Phi_3 \times \Delta t}$	Φ_1, Φ_2	-20889.18	0
$dissimilarity\ (\Delta t) = \mathbf{\Phi_1} + (\Phi_2 - \mathbf{\Phi_1}) \times e^{-\mathbf{\Phi_3} \times \Delta t}$	Φ_1, Φ_3	did not converge	--
$dissimilarity\ (\Delta t) = \Phi_1 + (\mathbf{\Phi_2} - \Phi_1) \times e^{-\mathbf{\Phi_3} \times \Delta t}$	Φ_2, Φ_3	-20887.45	1.73
$dissimilarity\ (\Delta t) = \mathbf{\Phi_1} + (\mathbf{\Phi_2} - \mathbf{\Phi_1}) \times e^{-\mathbf{\Phi_3} \times \Delta t}$	Φ_1, Φ_2, Φ_3	did not converge	--
$dissimilarity\ (\Delta t) = \Phi_1 \times (1 - e^{-\Phi_3 \times \Delta t})$	--	-13772.28	7116.90
$dissimilarity\ (\Delta t) = \mathbf{\Phi_1} \times (1 - e^{-\Phi_3 \times \Delta t})$	Φ_1	-17939.02	2950.16
$dissimilarity\ (\Delta t) = \Phi_1 \times (1 - e^{-\mathbf{\Phi_3} \times \Delta t})$	Φ_3	-16146.79	4742.39
$dissimilarity\ (\Delta t) = \mathbf{\Phi_1} \times (1 - e^{-\mathbf{\Phi_3} \times \Delta t})$	Φ_1, Φ_3	did not converge	--

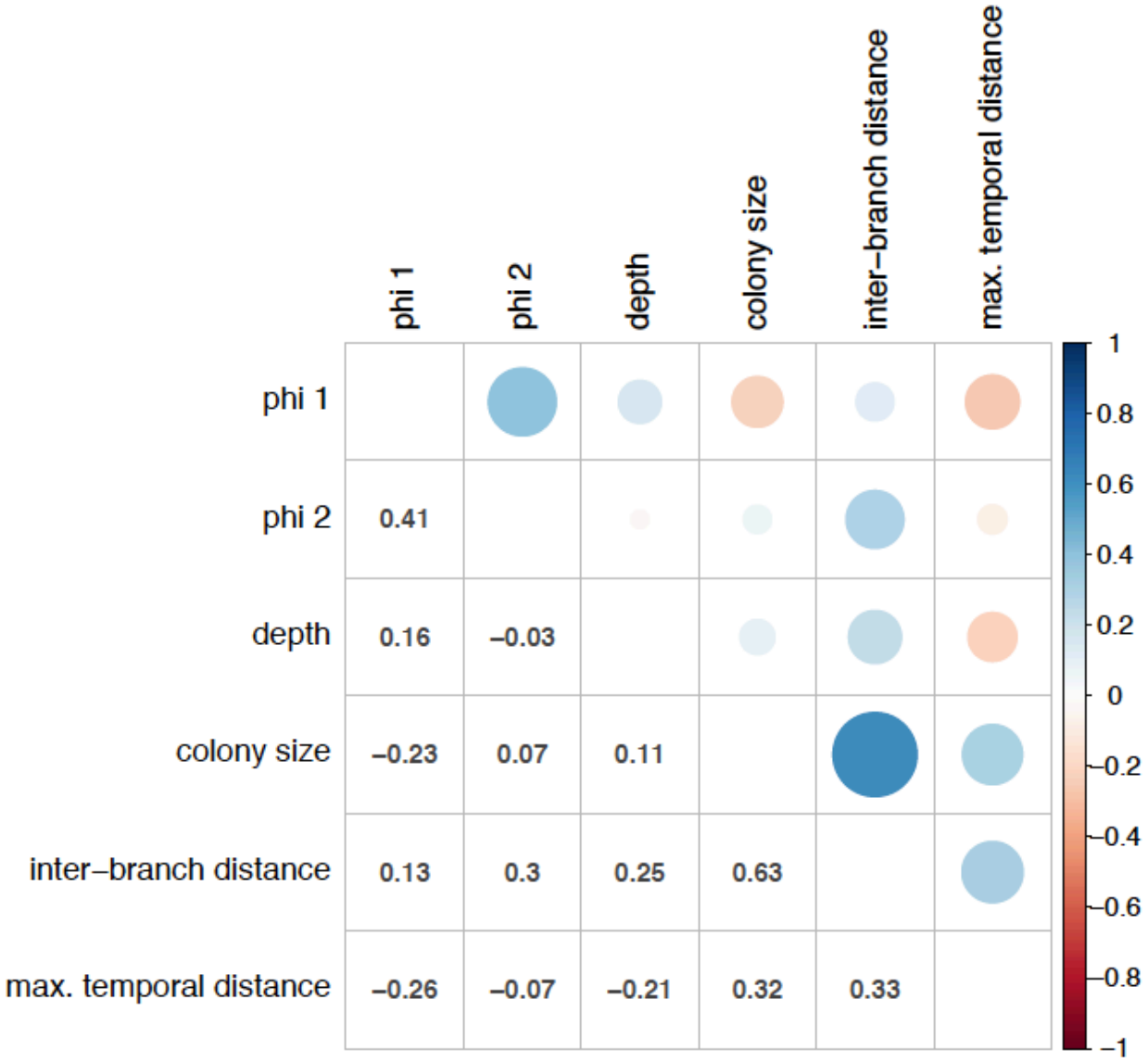

Figure 3.S1. Correlations between colony characteristics, i.e., depth, size, average inter-branch distance, and maximum temporal distance between surveys, and colony-specific model estimates for ϕ_1 and ϕ_2. Model estimates are from a nonlinear model of within-colony community dissimilarity over a temporal gradient. ϕ_1 predicts the asymptote for dissimilarity for within-community comparisons over increasingly long periods of time. ϕ_2 predicts the model intercept for dissimilarity within-community comparisons over negligible periods of time.

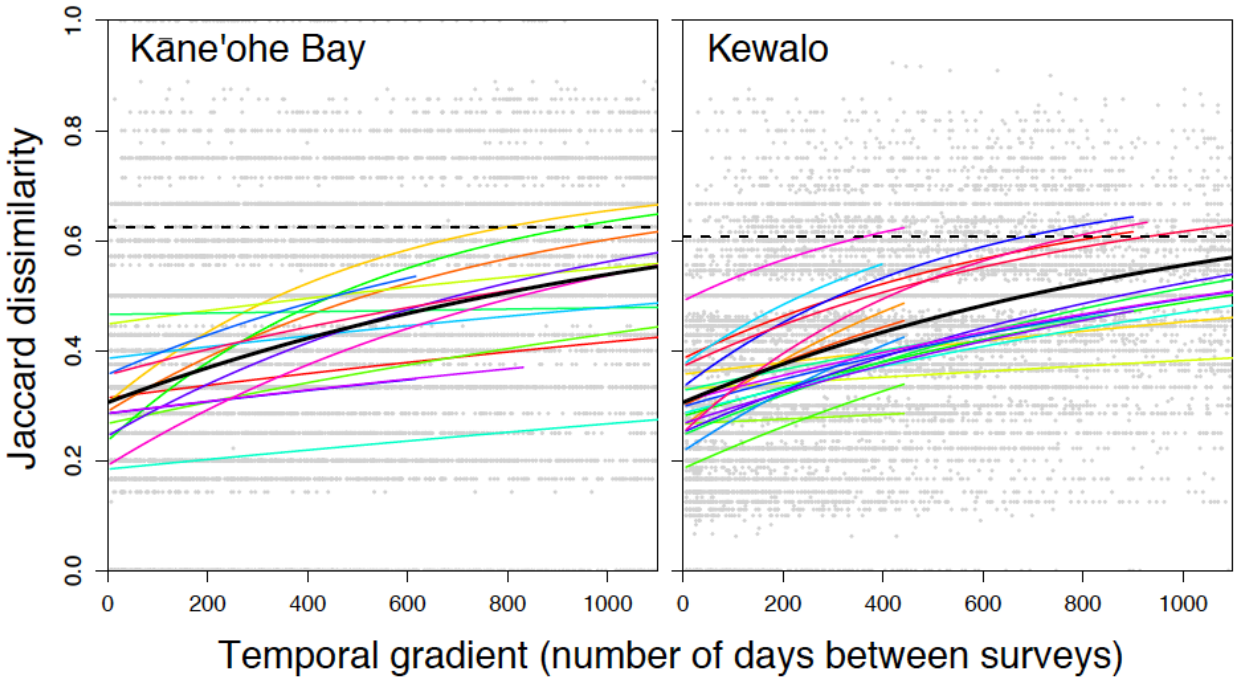

Figure 3.S2. Within-colony community dissimilarity (gray dots) across a temporal gradient is shown separately for communities at two survey sites. A non-linear model was used to estimate the rate of change, the intercept, and the asymptote for this relationship while allowing variation across individual colonies nested in sites for the model intercept and rate of change. The mean site-scale patterns are shown with a solid black line, and colony-scale trends are shown with multi-colored lines for colony-specific ranges along the temporal gradient. The average between colony spatial community dissimilarity for each site is shown with a black dashed line. This model had a similar model fit to the best model (ΔAIC = 1.73; Fig. 3.1).

CHAPTER 4

Priority effects and community assembly: effects of protection mutualists on coral reef cryptofauna

Abstract

Protection mutualists are often highly specialized for the foundation species that forms their preferred habitat, and they commonly display territorial behaviors as part of their protective services. When a guild of protection mutualist species coexists in the local environment, priority effects may inhibit the settlement of late arriving mutualists and other community members. Coral guard crabs (*Trapezia* spp.) and snapping shrimps (*Alpheus* spp.) rely on their host corals for food and shelter, and aggressively defend their hosts from coral predators. Previous studies have focused on the importance of these mutualist decapods for their host corals; in this study, we directly test how these species affect the coral-associated community. Specifically, we investigated whether *Trapezia* crabs and *Alpheus* shrimps affect the colonization and/or establishment of the community associated with their host corals using a two-stage factorial experiment. Established pairs of *Tr. intermedia* and *A. lottini* both had species-specific effects on the probability of colonization. *A. lottini* had strong inhibitory effects on conspecifics and limited colonization by some commensal and facultative species. *Tr. intermedia* did not affect colonization by other protection mutualists, but did inhibit colonization by xanthid and portunid crabs, as well as by a commensal shrimp species. *Tr. intermedia* and *A. lottini* continued to have species-specific effects on establishment success when community trajectories were monitored for six months. The inhibitory effects of these mutualist species constrained community composition through time, and a similar pattern was depicted in surveys of naturally occurring communities. Over six months of community assembly, initial treatments of *Tr. intermedia* and/or *A. lottini* explained 39% of variation in community composition. Host corals experimentally manipulated to have both *Tr. intermedia* and *A. lottini* had lower growth rates than corals with neither mutualist or with only *Tr. intermedia*, suggesting context dependency of the benefit of these mutualists to the host coral in the absence of corallivores.

Introduction

A fundamental goal of community ecology is to understand the assembly processes that drive variability in community composition. Priority effects occur when the order in which species arrive to a community affects the occurrence of subsequent colonizers and their ability to become established. Early arriving species can affect subsequent community assembly dynamics through either modification of available resources or species interactions that decrease (inhibitory effects) or increase (facilitative effects) the fitness of late arriving species. By affecting colonization and establishment rates, species that cause priority effects can strongly affect community level parameters, such as species richness, beta diversity, and productivity (Burkle and Belote 2015). For example, ants on wild cotton have inhibitory priority effects that alter the composition of the arthropod assemblage, decreasing community richness and evenness by 20% (Rudgers et al. 2010). Similarly, predatory and territorial reef fish species can have inhibitory priority effects that result in more variable reef fish communities with lower species richness and abundance (Shulman et al. 1983; Almany 2003, 2004; Martin and Wilsey 2012; Stier et al. 2013; Stier and Leray 2014). These effects on community level parameters are ultimately due to species-specific interactions, which may lead to varying outcomes for different functional groups within a community.

Strong priority effects are expected when one species is the prey of another, when species have high niche overlap, when the species that arrives first has a high impact on the habitat, or when the species that arrives second has specific resource requirements (Fukami 2015). These conditions are found in plant communities that rely on the availability of critical shared resources (i.e., space, light, nutrients, and water), which are often substantially modified by early arriving species (Lichter 1998, 2000). In plant communities priority effects can lead to distinct patterns of species turnover with the arrival and establishment of some species being inhibited and others being facilitated by the resource modifications of the early arriving species (Connell and Slatyer 1977; Ejrnæs et al. 2006; Burns et al. 2010; Burkle and Belote 2015).

Strong priority effects are expected when a foundational species has protection mutualists, because the habitat provided by the host species is a critical resource for the mutualists. If there is a guild of possible mutualists for a particular foundation species, then there is high potential for strong priority effects given high niche overlap, interactions between the

early arriving mutualist and the host habitat, and specific resource requirements of late arriving mutualists. Early arriving mutualist species may also affect the arrival and establishment of other species on the host through habitat modifications or through their protective relationship with the host. The magnitude of these priority effects on commensal species is expected to be smaller than those on other host mutualists due to lower niche overlap. The expected strength of priority effects is further diminished for species that have a facultative association with the host species given their low specificity of resource requirements relative to the foundational species.

Protection mutualism and the effects of the mutualist on other species associated with the host have been well studied in the ant-acacia system. Individual acacia trees generally host only one protection mutualist species from a guild of potential species (Janzen 1966). This system exhibits strong priority effects among the mutualist ant species whereby the first species to become established on the host can exclude the others (Palmer et al. 2002). When the least aggressive competitor ant species arrives to the acacia first, it imposes inhibitory priority effects by destroying leaf nectaries, which decreases the habitat quality for the other more aggressive ant species, thereby preventing colonization and takeover (Palmer et al. 2002). In addition to the ants having high niche overlap and a high impact on the host habitat, these protection mutualists also have specific resource requirements of shelter and food provided by the acacia tree, further strengthening priority effects within this system. The aggressive behavior of these protection mutualist ants can deter other guilds from associating with the acacia host including large herbivores (Janzen 1966) and potential pollinators (Raine et al. 2002). As exemplified by the ant-acacia system, the communities associated with a foundational species that has protection mutualists are likely to experience strong priority effects.

Coral guard crabs (*Trapezia* spp.) and snapping shrimps (*Alpheus* spp.) are protection mutualists that defend their host coral from predators in return for shelter and food, i.e., coral mucus (Pratchett 2001; McKeon et al. 2012; McKeon and Moore 2014; Rouzé et al. 2014). These species exhibit aggressive territorial behavior (Preston 1971; Gotelli and Abele 1983; Stewart et al. 2006; Schmitt et al. 2009; Stier et al. 2012; Britayev et al. 2017) and are common in *Pocillopora* coral associated communities (Preston 1971; Counsell et al. 2018). However, little is known about whether these species affect community assembly processes on their host coral. It is reasonable to expect that other species are able to distinguish between host corals with

and without trapeziid crabs and alpheid shrimps because these protection mutualists generate distinct audible signals (Au and Banks 1998; Pratchett 2001; Rouzé et al. 2014). The invertebrates associated with the branching cauliflower coral *Pocillopora meandrina* in Hawai‘i comprise a diverse community that includes five trapeziid crabs and two alpheid shrimps, in addition to a variety of commensal species that are commonly associated with pocilloporid corals and a broad range of facultative species that are observed throughout reef habitat and occasionally associated with these corals (Counsell et al. 2018). Analyses of community composition patterns have shown that *Tr. intermedia* has a unique distribution compared to the four other trapeziid crabs (Counsell et al. 2018), which may be the result of inhibitory priority effects.

Here we investigated whether protection mutualists affect the formation of the community associated with their host coral using a two-stage factorial experiment focused on *Tr. intermedia* and *A. lottini*. We hypothesized that colonizing species within the same guild as the established mutualist would experience strong inhibitory priority effects as a result of high niche overlap. We expected that commensal and mutualistic species from different families would experience moderate inhibitory priority effects due to the protective behaviors of established mutualists and some niche overlap, while facultative species would be negligibly affected due to relatively low niche overlap with mutualists. To quantify the effect of *Tr. intermedia* and *A. lottini* on colonization frequency, we followed the arrival of invertebrates to host corals with and without established mutualists. Then, to measure the persistence of priority effects, we tracked the communities associated with host corals for six months. We expected to see a continuous effect on the community through time, with guild-specific patterns in the establishment success of late arriving species similar to those hypothesized for colonization frequency. However, we were unsure whether the effects would intensify through compounding colonization successes and failures, or weaken through the dilution of species interactions across a growing community. To characterize potential long-term effects, we analyzed patterns in naturally occurring communities with and without *Tr. intermedia* and *A. lottini*. During both the colonization and establishment experiments, we tracked host coral growth. Previous studies by other researchers have focused on the importance of mutualist decapods for their host corals, ours is among the first to directly test how these species affect the coral-associated community.

Methods

Study Site

Forty *P. meandrina* colonies with naturally occurring pairs of *Tr. intermedia* were collected (State of Hawai‘i, Department of Land and Natural Resources, Division of Aquatic Resources Special Activity Permit for the Hawai‘i Institute of Marine Biology 2019-16) from the forereef of Kāne‘ohe Bay (~10.5 m depth, 21.4727786°N, -157.77934°W, Fig. 4.1a) and moved 2.6 km to a site on the southern side of Kāne‘ohe Bay (21.4511988°N, -157.7902512°W, Fig. 4.1a) in May 2016. The experimental site was ~3 m deep and next to a reef with naturally occurring *P. meandrina*. Corals were epoxied (Z-Spar Splash Zone Epoxy, A-788) to a polyvinyl chloride (PVC) plate (opaque gray, standard tolerance, ASTM D1784, 15.24 × 30.48 × 0.635 cm), buoyant weighed, and then outplanted to the experimental array. The corals were mounted to the top of standard cored concrete blocks (19.37 × 19.37 × 39.69 cm) using velcro straps through holes that were drilled in the concrete blocks and the PVC plates. Corals were aligned in four columns of ten, running parallel to the naturally occurring reef and were at least 10 m from the natural reef structure and 5 m from each other (Fig. 4.1b).

Experimental Design

Each coral was assigned to one of four treatments: (1) control without *Alpheus* shrimp or *Trapezia* crabs, (2) a pair of *A. lottini*, (3) a pair of *Tr. intermedia*, or (4) pairs of both *A. lottini* and *Tr. intermedia*. To establish these experimental treatments, each coral was brought to the surface and soaked for one minute in a dilute clove oil seawater mixture (0.0125% clove oil, a commonly used marine anesthetic, e.g., Holbrook and Schmitt 2002, Durville and Collet 2005, Cunha and Rosa 2006, Boyer et al. 2009, Hixon et al. 2012, Stier and Leray 2014), and all invertebrates were removed using bamboo skewers and/or tweezers. Because *A. lottini* and *Tr. intermedia* have a strong tendency to occur in heterosexual pairs (Coles 1980; McKeon et al. 2012) (Fig. 4.S1a & 4.S1b) and to reduce the risk of *A. lottini* and *Tr. intermedia* abandoning their coral after manipulation, naturally occurring pairs were kept together after removal and were returned to the host coral from which they were removed, according to the treatment randomly assigned to the coral. This approach limited the randomization of those treatments including *A. lottini* to the 24 corals that had a naturally occurring pair of *A. lottini*. All collected

corals had a pair of *Tr. Intermedia*, so *Tr. intermedia* had no effect on randomization of treatments. All pairs of *Tr. intermedia* removed from corals consisted of one male and one female crab. Corals were randomly assigned to a location in the experimental array blocked by row, such that each row of four corals contained one coral with each treatment, i.e., a randomized block design (Fig. 4.1b). As a result of logistical challenges in establishing the treatments, one colony that was initially assigned to be in the *A. lottini* treatment was shifted to the *Tr. intermedia* treatment; therefore, one row in the experimental array contains two *Tr. intermedia* treatment colonies and does not have an *A. lottini* treatment colony.

Colonization

To quantify the effects of established pairs of *A. lottini* and *Tr. intermedia* on colonization, corals were surveyed for colonists every other day for 62 days (June 18 to August 19, 2016). During each survey, the presence of established species appropriate for each coral's treatment was confirmed, and all colonizing invertebrates were counted and identified. Once a week, colonizing invertebrates were removed by bringing the corals to the surface in a mesh-lined bin and submersing the corals for one minute in a 0.0125% clove oil solution on the boat. Colonizing invertebrates that did not come off by agitating the coral in the clove oil solution were removed with bamboo skewers and/or tweezers. *A. lottini* and *Tr. intermedia* treatments were persistent throughout this two-month experiment.

Colonization was analyzed on a weekly basis: a colonizing species was counted only the first time it was observed before the weekly removal such that each species of colonizer could occur up to eight times (i.e., once per week) on each coral. The analysis was restricted to colonizing decapods, which were the most common colonizers and had strong potential for functional overlap with *A. lottini* and *Tr. intermedia*. Species that colonized with high frequency were analyzed individually, while species that colonized infrequently were grouped together based on genus (e.g., xanthid crabs) or guild (e.g., facultative species). Using generalized linear mixed models, GLMMs (function "glmer" in *R* package *lme4*; Bates et al. 2015), analyses of deviance with binomial error distributions and a logit link function were conducted to quantify the effects of *A. lottini* and *Tr. intermedia* treatments on the occurrence of colonizers, i.e., number of weeks arrived on each colony out of eight possible weeks. Treatment and colony size (initial dry weight based on buoyant weight measurements) were included in the model as fixed

effects, and row in the experimental array (block) was included as a random effect. Coral growth rate (methods described in the 'coral growth' subsection) and the interaction between treatment and colony size were included in initial models but were not significant for any of the colonizer species and were not examined further. For models in which treatment had a significant effect on colonizer occurrence, a *post hoc* analysis of estimated marginal means was used to determine which treatment pairs were distinct (function "emmeans" in *R* package *emmeans*; Lenth et al. 2018).

Establishment

To quantify the effects of pairs of *A. lottini* and *Tr. intermedia* on the establishment of colonizing species and to identify longer-term effects on community composition, the 40 experimental corals were tracked for six months allowing natural colonization and community assembly. Experimental treatments were reset at the start of the establishment experiment on August 28, 2016. Communities were surveyed weekly for six weeks and then monthly from October 20, 2016 to February 8, 2017. Treatments remained consistent during this six-month window with two exceptions: between weeks 4 and 5, the pair of *Tr. intermedia* from a *Tr. intermedia* treatment coral emigrated to an *A. lottini* treatment coral, and between months 5 and 6, the pair of *Tr. intermedia* from a *Tr. intermedia* treatment coral emigrated to a control treatment coral. In analyses, these two corals that lost their treatment *Tr. intermedia* were considered as *Tr. intermedia* treatment corals for the entire study period, and the two treatment pairs of *Tr. intermedia* that emigrated to other corals were considered as colonizers. These were the only *Trapezia* crabs with carapace lengths >1.0 cm observed as colonizers throughout the study; all other colonizing *Trapezia* had carapace lengths ≤0.5 cm when they were first observed.

To quantify the effects of *A. lottini* and *Tr. intermedia* treatments on the occurrence and persistence of species, GLMMs were used to conduct analyses of deviance in the occurrence of each species across treatments, sampling periods, and the interaction between treatment and sampling period, with coral individual included as a random effect. The number of weeks since the start of the establishment experiment was used as a discrete numeric variable for sampling period, and this measurement was centered and scaled prior to inclusion in models. Abundance data were used with a Poisson distribution for *Harpiliopsis depressa*, a species that was frequently observed on most corals (Table 4.S1), while presence/absence data were used with a

binomial distribution for all other species. Prior to analysis, some of these less frequently observed species were grouped together based on genus or guild comparable to the approach taken for the colonization data. For models in which treatment was significant, a *post hoc* analysis of estimated marginal means was used to determine which treatment pairs were distinct.

To analyze the effect of established pairs of *A. lottini* and *Tr. intermedia* on community structure through time (from week 1 to month 6), species richness, pairwise community dissimilarity, and decapod community composition were compared across treatments. Differences in these community level parameters were considered for the full community, including the pairs of *A. lottini* and *Tr. intermedia* that were on the coral at time 0 as treatments. For species richness, a GLMM was run with colony size (dry weight from buoyant weight at end of colonization experiment; centered and scaled), treatment, sampling period, and a treatment by sampling period interaction as fixed effects. This model included coral individual as a random effect and used a Poisson error distribution. To examine whether treatments constrained community assembly, the Jaccard community dissimilarity index was calculated for all colony pairs within each treatment group at each sampling period (function "vegdist" in *R* package *vegan*; Oksanen et al. 2017). These dissimilarity values were normally distributed. To determine whether communities had different dissimilarities across treatments and through time, a linear mixed model was run with treatment, sampling period, and the interaction of these variables as fixed effects. This model included the identity of unique coral pairs as a random effect to account for repeated measures. For the species richness and community dissimilarity models, if treatment was significant, then *post hoc* analyses of estimated marginal means were used to determine which treatment pairs were distinct.

Variation in community composition through time was compared between treatments using permutational multivariate analyses of variance, PERMANOVA (function "adonis" in *R* package *vegan*; Oksanen et al. 2017), with 10,000 permutations of Bray-Curtis distance matrices calculated after using Wisconsin double standardization of species abundance matrices. PERMANOVAs were run for each time step separately to quantify the amount of variation explained by treatments at each time step. In addition, a PERMANOVA was run for all communities through time (from week 1 to month 6) including treatment, sampling period, and an interactions term. Permutations were constrained within coral individuals to account for

repeated measures on each coral. Non-metric multidimensional scaling, NMDS (function "metaMDS" in *R* package *vegan*; Oksanen et al. 2017), was used to produce an ordination of community dissimilarities across treatments and sampling periods.

Naturally Occurring Communities

To relate our experimental results to naturally occurring decapod communities, species richness, pairwise community dissimilarity, and community composition were calculated on naturally occurring *P. meandrina* surveyed around the island of O'ahu from 2013 to 2017 (Counsell et al. 2018). The naturally occurring colonies were restricted to 15.1 to 25.4 cm diameter (the size range of the experimental corals) and >50% live coral tissue. For comparison to the experimental treatments, these corals (n=321) were divided into groups based on the occurrence of *Tr. intermedia* (104 corals), *A. lottini* (62 corals), both (92 corals), or neither (63 corals) (Fig. 4.S1c). Differences among these groupings were analyzed for the full decapod community. Using a generalized linear model (function "glm" in *R* package *stats*; R Core team) with Poisson error distribution, species richness was compared between groups with coral size as a covariate. The Jaccard dissimilarity index was calculated for all community pairs within each group, and an analysis of variance, ANOVA (function "aov" in *R* package *stats*; R Core team), was used to test for differences in dissimilarity across groups. For both species richness and community dissimilarity analyses, Tukey's honest significant differences method (function "TukeyHSD" in *R* package *stats*; R Core team) was used to determine significant pairwise differences between groups. In addition, a PERMANOVA was run with 10,000 permutations of Bray-Curtis distance matrices using the Wisconsin double standardization of species abundance matrices to determine how much variation in community composition could be accounted for by groups. NMDS was used to visualize community composition dissimilarities across treatments.

Coral Growth

To monitor coral growth, corals were buoyant weighed (Jokiel et al. 1978) at the beginning (June 7-14, 2016) and at the end (August 15-19, 2016) of the 8-week colonization experiment. For the 6-month establishment experiment, coral growth was calculated using each colony's longest length and longest orthogonal width from photographs at the beginning and end of the establishment experiment. For both experiments, colony growth was calculated as the

difference between final and initial colony size as a percent of the initial colony size. The relationship between coral colony growth rate and community treatment was analyzed using linear regressions with initial colony size included in the model as a covariate (function "lm" in *R* package *stats*; R Core team). For the model of coral growth during the colonization experiment, the numbers of air and clove oil exposures were also included as covariates.

Results

Colonization

Six species known to be *P. meandrina* trapeziid and alpheid mutualists colonized the corals: *Tr. bidentata*, *Tr. digitalis*, *Tr. intermedia*, *Tr. tigrina*, *A. lottini*, and *Synalpheus charon* (Table 4.S1). *A. lottini* colonizers occurred with a lower frequency on *A. lottini* treatment corals, while *S. charon* did not respond to either the *A. lottini* or *Tr. intermedia* treatment (Table 4.1, Fig. 4.2). For *Tr. intermedia* and the other three trapeziid crabs, there was no effect of treatment on probability of occurrence (Fig. 4.2), but probability of occurrence did increase with colony size (Table 4.1, Fig. 4.S2). Colonizers considered to be commensal with *P. meandrina* included three species of xanthid crabs, i.e., *Domecia hispida, Etisus demani*, and *Pseudoliomera speciosa*, and the flattened coral shrimp *Harpiliopsis depressa* (Table 4.S1). The xanthid crabs and *H. depressa* had a higher probability of occurrence on control corals than corals with *A. lottini* and/or *Tr. intermedia* (Table 4.1, Fig. 4.2). *H. depressa* was an order of magnitude more likely to occur than all of the other commensal and mutualist species (Table 4.S1).

Colonizing facultative species included hermit crabs, mantis shrimps, rock crabs, and portunid crabs (Table 4.S1). The portunid crab *Thalamita coerulipes* was observed at a high frequency, comparable to *H. depressa* (Table 4.S1), and was therefore analyzed separately from the other facultative species. *Th. coerulipes* was observed more frequently on control corals than corals with *A. lottini* and/or *Tr. intermedia* treatments (Table 4.1). The occurrence of *Th. coerulipes* was also significantly lower on corals with *Tr. intermedia* than on corals with only *A. lottini*. For the remaining facultative species, there was no effect of treatment on the probability of colonization (Table 4.1, Fig. 4.2).

Establishment

The probability of occurrence increased significantly through time for *A. lottini*, *Tr. intermedia*, other trapeziid crabs, and the grouped facultative species (Table 4.2). The overall trend through time was not significant for *H. depressa* or xanthid crabs. *Th. coerulipes* was the only taxon to have a significant decrease in occurrences through time (Table 4.2, Fig. 4.3).

A. lottini was observed more often and with increasing abundance on corals without *A. lottini* (Table 4.2, Fig. 4.3). The other alpheid shrimp observed, *S. charon*, was observed only once on each of three corals (two corals with treatment *A. lottini* and *Tr. intermedia*, and one *Tr. intermedia* treatment coral) throughout the community establishment experiment. *Tr. intermedia* was observed with low frequency (Table 4.S1) and showed no difference among treatments (Table 4.2, Fig. 4.3). The other trapeziid crabs (i.e., *Tr. tigrina* and *Tr. digitalis*) were observed more often and showed higher persistence through time on corals without *Tr. intermedia* (Table 4.2, Fig. 4.3). The commensal *H. depressa* was observed with notably higher frequency than any other species and was established on all but one coral at month six (Table 4.S1, Fig. 4.3). There was no difference in the abundance of *H. depressa* among treatments or across sampling periods (Table 4.2). While the probability of occurrence was not significantly different among treatments for xanthid crabs (i.e., *D. hispida* and *E. demani*), most of the observations of xanthid crabs were on control corals, and xanthid crabs had significantly different trajectories among treatments (Table 4.2, Fig. 4.3). The portunid crab *Th. coerulipes* was observed most often on control corals, followed by corals with *A. lottini*, and least often on corals with *Tr. intermedia* or with *A. lottini* and *Tr. intermedia* (Table 4.2, Fig. 4.3). Further, the probability of *Th. coerulipes* occurrence declined faster on control corals and corals with *Tr. intermedia* (Table 4.2, Fig. 4.3). Other facultative species (i.e., mantis shrimps and hermit crabs) were observed more often on control corals than on corals that had both *A. lottini* and *Tr. intermedia*, and at intermediate levels of observation on corals with either *A. lottini* or *Tr. intermedia* (Table 4.2, Fig. 4.3).

Species richness increased through time for all corals ($p < 0.001$), but was not different relative to treatments or the interaction of sampling time and treatment (Table 4.3, Fig. 4.4a). A similar pattern was observed for species abundance (Fig. 4.S3). Dissimilarity between communities increased through time for all treatments ($p < 0.001$) and was different among treatments ($p < 0.001$). Different treatments also showed different trajectories for community

dissimilarity through time ($p < 0.001$). Corals from the control group and corals that started with a pair of *A. lottini* had the highest community dissimilarities (no difference between these two treatments, $p = 0.102$), corals that started with a pair of *Tr. intermedia* had a moderate level of community dissimilarity, and corals that started with both *A. lottini* and *Tr. intermedia* had the lowest community dissimilarity (Table 4.3, Fig. 4.4b). Corals from the control group had a more rapid change in community dissimilarity than corals from the other treatments, with corals that had both *A. lottini* and *Tr. intermedia* displaying almost no change in dissimilarity through time.

Treatment was a significant predictor of variation in community composition at each sampling period ($p < 0.001$) with the amount of variation explained declining from 100% at the beginning of the experiment to 20% after six months of community assembly (Fig. 4.4c). When all sampling times (except week 0) were considered in a single PERMANOVA, treatment accounted for 39% variation in community composition, sampling time accounted for 8% variation, and differences in the trajectory of treatments through time accounted for 3% variation (Table 4.3). NMDS plots through sampling times showed some convergence in community composition across treatments through time (Fig. 4.S4). Corals with both *A. lottini* and *Tr. intermedia* had the smallest spread in multidimensional space, followed by corals with either *A. lottini* or *Tr. intermedia*, and control corals had the largest spread (Fig. 4.S4).

Naturally Occurring Communities

The naturally occurring decapod communities on corals with *A. lottini* only, *Tr. intermedia* only, both, or neither differed in species richness ($p < 0.001$) such that each grouping had a different mean species richness than each of the other groupings ($p < 0.05$ for all pairwise comparisons). Communities with both *A. lottini* and *Tr. intermedia* had the highest species richness, followed by corals with *A. lottini*, then corals with *Tr. intermedia*, and finally corals with neither *A. lottini* nor *Tr. intermedia* (Table 4.3, Fig. 4.4a). Dissimilarity between communities was different across groupings ($p < 0.001$) such that each grouping had a different mean dissimilarity index than each of the other groupings ($p < 0.001$ for all pairwise comparisons). Dissimilarity was the lowest on corals with both *A. lottini* and *Tr. intermedia*, followed by corals with *Tr. intermedia*, then corals with *A. lottini*, and dissimilarity was the highest on corals with neither *A. lottini* nor *Tr. intermedia* (Table 4.3, Fig. 4.4b). A similar pattern was depicted in an NMDS plot of the composition of natural communities (Fig. 4.S4).

The groupings based on the presence of *A. lottini*, *Tr. intermedia*, both, or neither accounted for 44% of the variation in the composition of naturally occurring communities (PERMANOVA, Table 4.3, Fig. 4.4c).

Coral Growth

During the colonization experiment, coral growth rates were lower in the *A. lottini* and *Tr. intermedia* corals than in control corals (p=0.05) or *Tr. intermedia* corals (p=0.03) (Fig. 4.5). Growth rates of *A. lottini* corals were similar to those of control and *Tr. intermedia* corals; however, they were not significantly different than the growth rates of corals with both *A. lottini* and *Tr. intermedia*. During the establishment experiment, coral growth rates did not differ among treatments (p=0.15, Fig. 4.S5).

Discussion

These results indicate the importance of priority effects on decapod communities associated with *P. meandrina*. There were species-specific inhibitory effects from *A. lottini* and *Tr. intermedia* at both the colonization (Fig. 4.2) and establishment stages (Fig. 4.3) of community assembly. These species-specific effects were persistent through time and corresponded with community level differences, particularly in the variety of species in communities, which aligned with patterns observed in naturally occurring communities (Fig. 4.4).

Given high niche overlap among species in the same guild, both *A. lottini* and *Tr. intermedia* were expected to have strong priority effects through aggressive territorial behaviors towards other protection mutualist species (Huber 1987; Fukami 2015). *A. lottini* almost entirely prohibited the colonization and establishment of conspecifics. On corals without treatment *A. lottini*, *A. lottini* individuals were frequently observed as colonizers and were able to become established as observed through their persistence through time (Fig. 4.2 & 4.3). Despite strong competitive exclusion of conspecifics, *A. lottini* had no effect on the other alpheid shrimp observed, *S. charon*, which colonized corals with and without treatment *A. lottini* (Fig. 4.2). Alternatively, *Tr. intermedia* did not affect the colonization or establishment of conspecifics, which were observed across all treatments with low frequency (Fig. 4.2 & 4.3). *Tr. intermedia* did restrict the establishment of other trapeziid crabs, which colonized corals across all

treatments (Fig. 4.2) but were able to become established only on corals without an established pair of *Tr. intermedia* (Fig. 4.3). Late arriving *Tr. intermedia* were observed in both the colonization and the establishment experiments, but they did not persist on corals of any treatment (Fig. 4.3). These results suggest that when *Tr. intermedia* is the first trapeziid species to arrive to a coral and has time to become established, it can effectively keep other trapeziid species from becoming established on the coral. However, when *Tr. intermedia* arrives around the same time as other trapeziid crabs, the other species are able to exclude *Tr. intermedia* (Fig. 4.3). Further studies are needed to elucidate the competition-colonization tradeoff dynamics among trapeziid crabs. Priority effects were not observed between *Tr. intermedia* and alpheid shrimps, nor between *A. lottini* and trapeziid crabs (Fig. 4.2 & 4.3). Previous studies have shown that mutualists from these two families can have synergistic defensive behaviors for the host coral (McKeon et al. 2012) and that some species pairs between these two families co-occur more often than expected by chance (Stier et al. 2012). Our results further suggest that protective mutualists from these two families do not have strong competitive interactions and may have complementary niches on host corals.

Both *A. lottini* and *Tr. intermedia* strongly inhibited the colonization of commensal decapods, such as the flattened coral shrimp *H. depressa* and xanthid crabs (Table 4.S1, Fig. 4.2). Despite having lower colonization frequency on corals with *A. lottini* and/or *Tr. intermedia*, *H. depressa* still had high colonization frequency relative to other species across treatments and was able to become established on almost every coral during the establishment experiment (Table 4.S1, Fig. 4.3). Variation in the abundance of *H. depressa* during the establishment experiment followed a similar pattern through time across all treatments suggesting a potential environmental driver of population dynamics for this species that operates at a larger spatial scale than that of the host coral (Fig. 4.3). Xanthid crabs continued to respond to the presence of protective mutualists during the establishment experiment, becoming established in notable abundances only on corals without *Tr. intermedia* (Fig. 4.3). Despite becoming established on control and *A. lottini* treatment corals, xanthid crab abundances on these corals declined about two months into the establishment experiment. This result suggests that the successful establishment of mutualist species on corals without experimentally established mutualist species

(Fig. 4.3) negatively affects the presence of commensal crabs, even if they arrive to the host coral at a similar time as the mutualist species.

The facultative decapod species observed were predominately the portunid crab *Th. coerulipes*, hermit crabs, and mantis shrimps (Table 4.S1). The high abundance of *Th. coerulipes* was surprising given the low abundance of portunid crabs in community surveys around O‘ahu (Counsell et al. 2018), and the higher frequency of portunid crabs on dead corals than on live pocilloporid corals in the Red Sea (Spiridonov and Neumann 2008). As expected for species that have low functional overlap with protection mutualists and do not have host-coral-specific resource needs, hermit crabs and mantis shrimps had low colonization frequency across all treatments (Fig. 4.2). However, inhibitory effects of *A. lottini* and *Tr. intermedia* were observed during the six month community establishment experiment as these facultative species became established more often on control corals than on corals that had both *A. lottini* and *Tr. intermedia*, with intermediate levels of establishment success on corals with either *A. lottini* or *Tr. intermedia* (Table 4.2, Fig. 4.3).

The portunid crab *Th. coerulipes* had colonization rates an order of magnitude higher than all other species except *H. depressa* (Fig. 4.2). While *H. depressa* is a commonly associated with pocilloporid corals, *Th. coerulipes* is not (Table 4.S1, Counsell et al. 2018). Both *A. lottini* and *Tr. intermedia* inhibited the colonization and establishment of *Th. coerulipes* (Fig. 4.2 & 4.3). Stronger inhibitory effects were observed in both experiments with *Tr. intermedia*, potentially because taxonomic and functional similarity is greater between portunid crabs and trapeziid crabs than between portunid crabs and alpheid shrimps. Despite high colonization rates and some signs of establishment on control corals and corals with only *A. lottini*, *Th. coerulipes* abundance decreased through time. This may reflect the ongoing establishment of alpheid shrimps and trapeziid crabs on corals that started without these species, suggesting that these species outcompete *Th. coerulipes* for this habitat regardless of order of arrival. This pattern, similar to that observed for xanthid crabs, supports a shift through time in the communities on control corals from generalist to specialist species, which may use the habitat and associated resources more efficiently (Belyea and Lancaster 1999).

The species-specific priority effects of *A. lottini* and *Tr. intermedia* on the decapod community associated with *P. meandrina* resulted in persistent differences in community

structure across treatments. The initial presence of pairs of *A. lottini* and/or *Tr. intermedia* accounted for 20% of the variation in community composition after six months (Fig. 4.4c). While species richness of the decapod community was not different among experimental treatments, community dissimilarity between corals within each treatment was different among treatments (Fig. 4.4a & 4.4b). Communities were the most similar, and therefore the most restricted, for corals that started with both *A. lottini* and *Tr. intermedia*, and the most dissimilar for the control corals that started without either mutualist (Fig. 4.S4). As was suggested by the stronger inhibitory effects of *Tr. intermedia* than of *A. lottini* on xanthid and portunid crabs, *Tr. intermedia* constrained the community composition more than *A. lottini* (Fig. 4.4b). The naturally occurring communities showed the same pattern in community dissimilarities, with the grouping of corals that had *A. lottini* exhibiting more variation in their community composition than the grouping of corals that had *Tr. intermedia* (Fig. 4.4b). The stronger restrictive effect on community composition of *Tr. intermedia* compared to *A. lottini* is also depicted in the species richness differences across the natural community groupings (Fig. 4.4a). The corals grouped as having *A. lottini* had one more species on average than corals grouped as having *Tr. intermedia* (Fig. 4.4a). Intriguingly, the species richness across all groupings was lower for the natural communities than for the experimental communities. This result may be due to the unique isolation of the experimental corals within a rubble field, or this may suggest that the experimental communities were still in fairly formative stages of community assembly with a higher proportion of generalist species than observed in natural communities.

Trapeziid crabs and alpheid shrimps are considered mutualists for their host coral as a result of protecting the coral from the deleterious effects of corallivorous sea stars (Pratchett 2001; McKeon et al. 2012; Rouzé et al. 2014) and vermetid snails (Stier et al. 2010), as well as removing sediments from the coral tissue (Stewart et al. 2006; Stier et al. 2012; Rouzé et al. 2014). During our experiment, corallivorous sea stars and vermetid snails were not observed within or around the experimental grid, so the strong mutualistic benefit of increased coral survival that has been observed in some studies was neither expected nor observed. Alternatively, our site, comparable to many sites within Kāneʻohe Bay, had high sediment-stress levels with accumulation noticeable on our experimental cement blocks every two days. A clear mutualistic benefit of increased coral growth was expected for colonies with either mutualist as a

result of sediment clearing services. Over the two-month colonization experiment, there was no difference in coral growth rates for corals without mutualists as compared to corals with either *Tr. intermedia* or *A. lottini* (Fig. 4.5). These results are similar to those from a previous study which found that trapeziid crabs increased coral growth rates only when corals were in the vicinity of vermetid snails (Stier et al. 2010). However, in addition to not observing an increase in coral growth for colonies with established mutualists, coral growth for colonies with both *Tr. intermedia* and *A. lottini* were actually lower than for colonies that had neither mutualist species or only *Tr. intermedia*. This pattern suggests a context dependency to these mutualisms in which the cost of producing extra coral mucus and specific fat bodies (Stimson 1990) as food for the mutualist crabs and shrimps is not always be balanced by the benefits of their housekeeping and protection services.

While we are not aware of this degree of context dependency being previously documented for trapeziid and alpheid mutualists, this switch from positive to negative feedbacks within a mutualistic relationship has been previously described in other systems. A study focused on a coral dwelling fish found that the fish can have positive or negative effects on the host coral depending on environmental conditions (Chase et al. 2014). Even the ant-acacia association may have a negative effect on the host tree where the cost of maintaining the ant mutualists through the production of nectar rewards is greater than the benefits of reduced chronic herbivore damage, as documented by trees with ants having reduced growth and reproductive output in the absence of highly destructive elephant browsing (Stanton and Palmer 2011). Future studies aiming to quantify the costs and benefits of trapeziid crabs and alpheid shrimps associations with pocilloporid corals in different environmental conditions would improve our understanding of these mutualisms.

Our results highlight the importance of community history for coral-associated reef communities by quantifying the effects of protective mutualists on the subsequent colonization and establishment of the same and other species, as well as on the overall community structure. In addition, our findings are consistent with previous studies that have shown that the strength of priority effects can vary for different species even when they represent comparable functional groups (Shulman et al. 1983; Almany 2003, 2004; Stier and Leray 2014). We observed strong and consistent competitive exclusion by trapeziid and alpheid mutualist for species from the

same guild, indicating potential colonization/competition tradeoff dynamics particularly for trapeziid crabs. The mutualist-to-mutualist inhibitory effects we recorded were generally limited to species from the same family suggesting complementary resource niches for coral protection mutualists from different families. Priority effects of protection mutualists were observed for species that have commensal and facultative relationships with the host, with the strongest inhibitory effects among brachyuran species, i.e., between trapeziid crabs and both xanthid and portunid crabs. The effects on commensal and facultative species varied as the communities formed through time, suggesting that these competitive dynamics may be deterministic as opposed to contingent on order of arrival. Protection mutualisms within coral-associated communities affected the community assembly process through species-specific inhibition of colonization and establishment dynamics. The effects of these dynamics on overall community composition persisted through time, indicating the importance of understanding priority effects as a driver of variation in community composition.

Table 4.1. Model output from binomial GLMs for the proportion of sampling days that colonizers were observed on corals. Treatment output (function "Anova" in *R* package *car*; Fox et al. 2018) and size output (function "summary" in *R* package *base*; Chambers and Hastie 1992) from models run with these two variables as fixed effects and grid row (i.e., treatment block) as a random effect. Significant results are bolded.

	Treatment			Colony Size			
Colonizer Type	LR X^2	df	Pr(>X^2)	Estimate	Std. Error	z value	Pr(>|z|)
Alpheus lottini	13.471	3	**0.004**	0.817	0.505	1.618	0.106
Synalpheus charon	2.788	3	0.426	0.286	0.347	0.826	0.409
Trapezia intermedia	1.734	3	0.629	0.682	0.333	2.048	**0.041**
Other trapeziid crabs*	2.429	3	0.488	0.732	0.288	2.546	**0.011**
Xanthid crabs*	8.716	3	**0.033**	0.636	0.502	1.268	0.205
Harpiliopsis depressa	13.574	3	**0.004**	0.063	0.135	0.463	0.644
Facultative decapod spp. (not including *Th. coeruilpes*)	0.640	3	0.887	0.131	0.444	0.296	0.767
Thalamita coeruilpes	128.818	3	**<0.001**	-0.456	0.223	-2.038	0.042

*Species details in Table 4.S1.

Table 4.2. Model output from GLMMs for community members on corals during a community establishment experiment (binomial distribution was used with presence/absence data, except for the models on *Harpiliopsis depressa* which used a Poisson distribution and abundance data). Output (function "Anova" in *R* package *car*; Fox et al. 2018) from models run with treatment (df=3), sampling time (the models do not include week zero as this week was defined by the experiment), and an interaction term (df=3) as fixed effects, and colony individual as a random effect. The marginal R^2 value (function "r.squaredGLMM" in *R* package *MuMIn*; Bartoń 2016) is an estimate of the variation explained by all fixed effects in the model. For *A. lottini* and *Tr. intermedia*, models run with the interaction term were nearly unidentifiable, so a model without the interaction is presented. Significant results are bolded.

	Treatment		Sampling Time			Treatment × Time		R^2_m
Community Member	LR X^2	Pr (>X^2)	Effect Estimate	LR X^2	Pr (>X^2)	LR X^2	Pr (>X^2)	
Alpheus lottini	18.82	**<0.001**	1.323	45.65	**<0.001**	na	na	0.98
Trapezia intermedia	1.50	0.681	0.914	19.65	**<0.001**	na	na	0.27
Other trapeziid crabs*	15.29	**0.002**	2.028	49.79	**<0.001**	10.56	**0.014**	0.41
Xanthid crabs*	5.80	0.122	-0.284	0.38	0.538	14.49	**0.002**	0.46
Harpiliopsis depressa	6.99	0.072	0.037	2.33	0.127	0.30	0.960	0.03
Facultative decapod spp. (not including Th. coeruilpes)	8.68	**0.034**	1.395	44.16	**<0.001**	3.72	0.294	0.48
Thalamita coeruilpes	35.20	**<0.001**	-1.217	8.20	**0.004**	15.49	**0.001**	0.61

*Species details in Table 4.S1.

Table 4.3. Model output for community level parameters relative to the decapod communities on corals manipulated (n=40) to have a pair of *A. lottini* or *Tr. intermedia*, both, or neither and then followed for six months (surveyed eleven times), and on naturally occurring corals surveyed around O'ahu (n=321, surveyed once). All models had the community level parameter as the response variable, treatment as a fixed effect, and for the models on experimental communities time and the interaction of time and treatment were also included as fixed effects. The GLMM for species richness of experimental communities included coral size as a covariate and coral individual as a random effect, and had a Poisson error distribution. The GLM for species richness of natural communities included coral size as a covariate and had a Poisson error distribution. The GLMM on the experimental community dissimilarities included unique coral pairs as a random effect (pairwise measures were repeated within treatments for each time step) and had a Gaussian error distribution. The GLM for natural community dissimilarities was a simple linear model with a Gaussian error distribution. Community matrices for the experimental and natural communities were Wisconsin double standardized prior to PERMANOVAs. For the experimental community PERMANOVA, permutations were constrained within individual coral colonies to account for repeated measures on each coral. Significant results are bolded.

Model Type (response variable)	Community	Treatment		Time		Treatment × Time	
GLMM (species richness)	Experimental	X^2 = 6.0	p = 0.113	X^2 = 29.0	p <**0.001**	X^2 = 1.1	p = 0.785
	Natural	X^2 = 56.2	p <**0.001**	(no time component)			
GLMM (Jaccard dissimilarity)	Experimental	X^2 = 307.7	p <**0.001**	X^2 = 289.8	p <**0.001**	X^2 = 53.3	p <**0.001**
	Natural	F value = 349.1	p <**0.001**	(no time component)			
Permanova (Bray Curtis distance)	Experimental	R^2 = 0.394	p <**0.001**	R^2 = 0.077	p <**0.001**	R^2 = 0.027	p <**0.001**
	Natural	R^2 = 0.437	p <**0.001**	(no time component)			

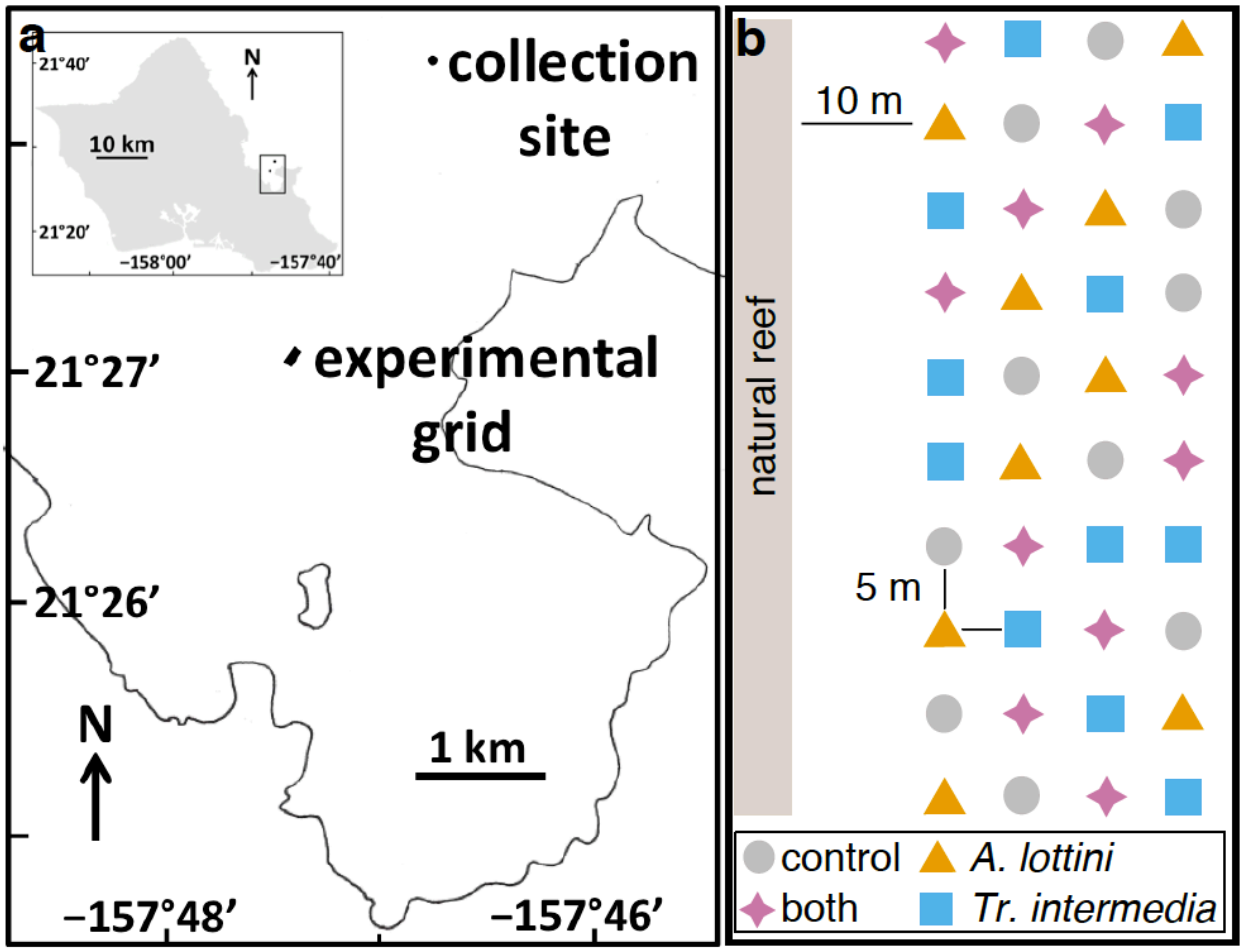

Figure 4.1. Inset map of the island of O‘ahu, Hawai‘i with study site outlined. (a) Location of experimental grid within Kāne‘ohe Bay relative to collection site. (b) Arrangement of experimental colonies with treatments blocked by row. Each coral was separated from its closest neighbors by 5 m of rubble, and the entire experimental grid was at least 10 m from natural reef structure.

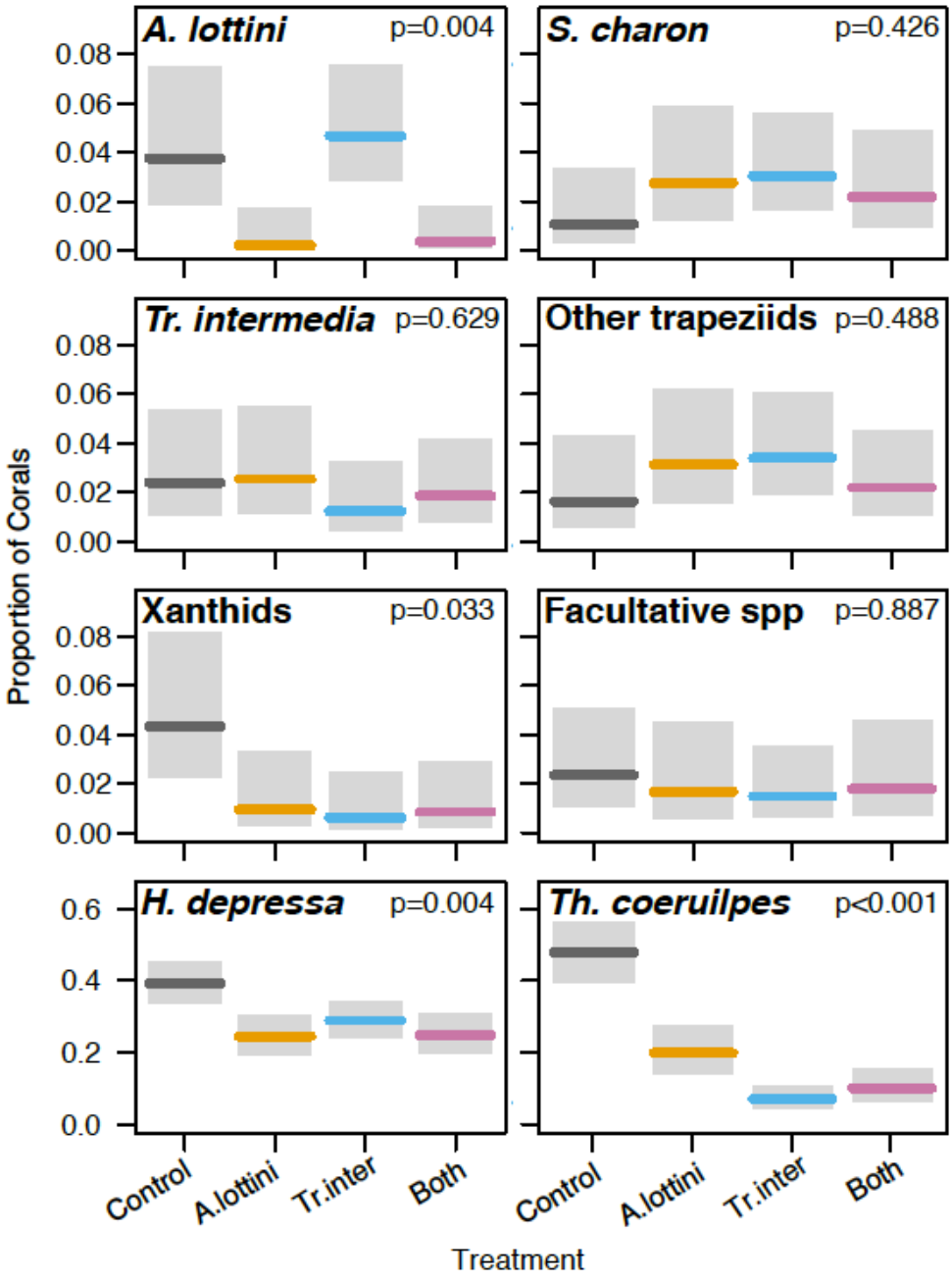

Figure 4.2. The average proportion of corals across treatment groups on which a colonizer type was observed with 95% confidence intervals (gray bars). Output is based on GLMMs that had the proportion of survey windows (considering each coral separately) with occurrence of each colonizer type as the response variable. Models included treatment and colony size (Fig. 4.S2) as fixed effects (Table 4.1), and treatment block (row, Fig. 4.1b) as a random effect. Treatment groups were control corals without mutualists, corals with a pair of *A. lottini*, corals with a pair of *Tr. intermedia*, and corals with pairs of both species.

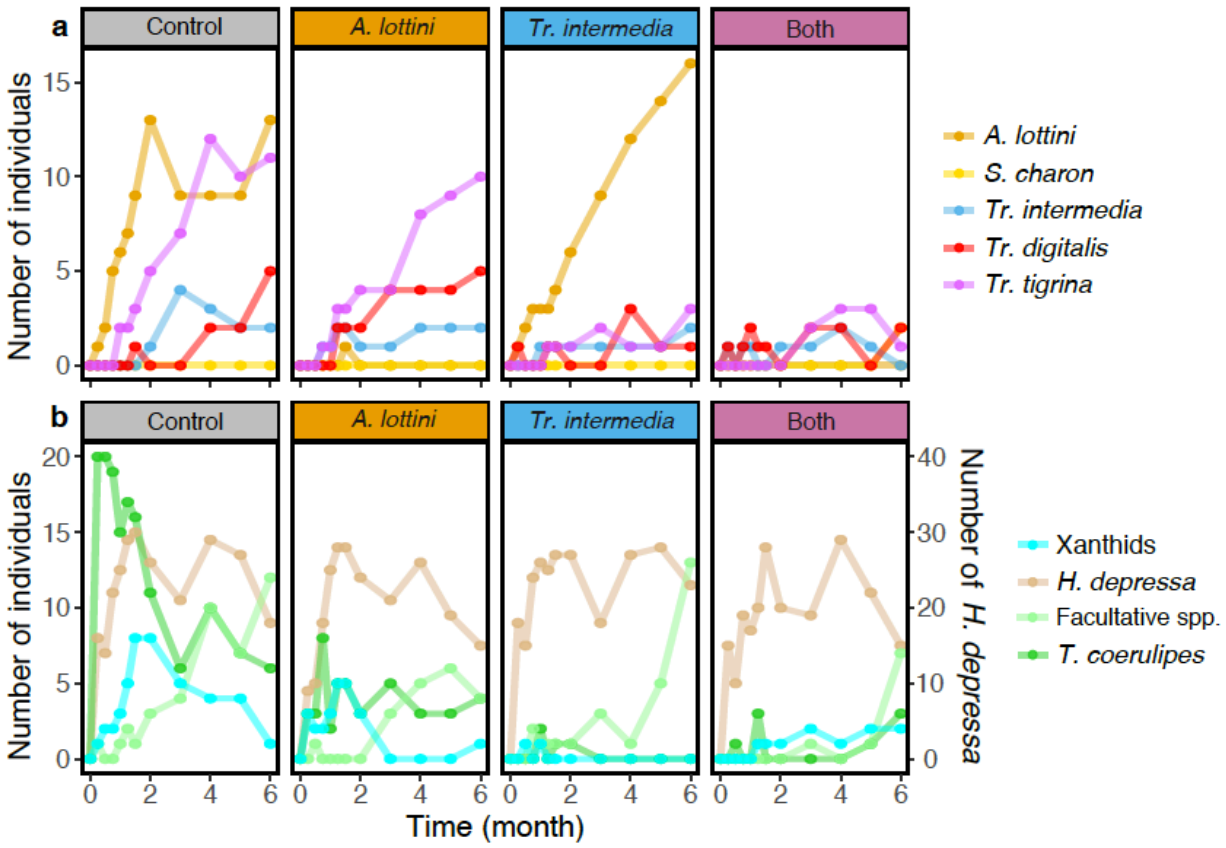

Figure 4.3. The number of individuals through time on all corals within each treatment. (a) The number of individuals from Trapeziidae and Alpheidae. (b) The number of commensal and facultative decapod individuals. Species details for xanthid crabs and facultative species are in Table 4.S1.

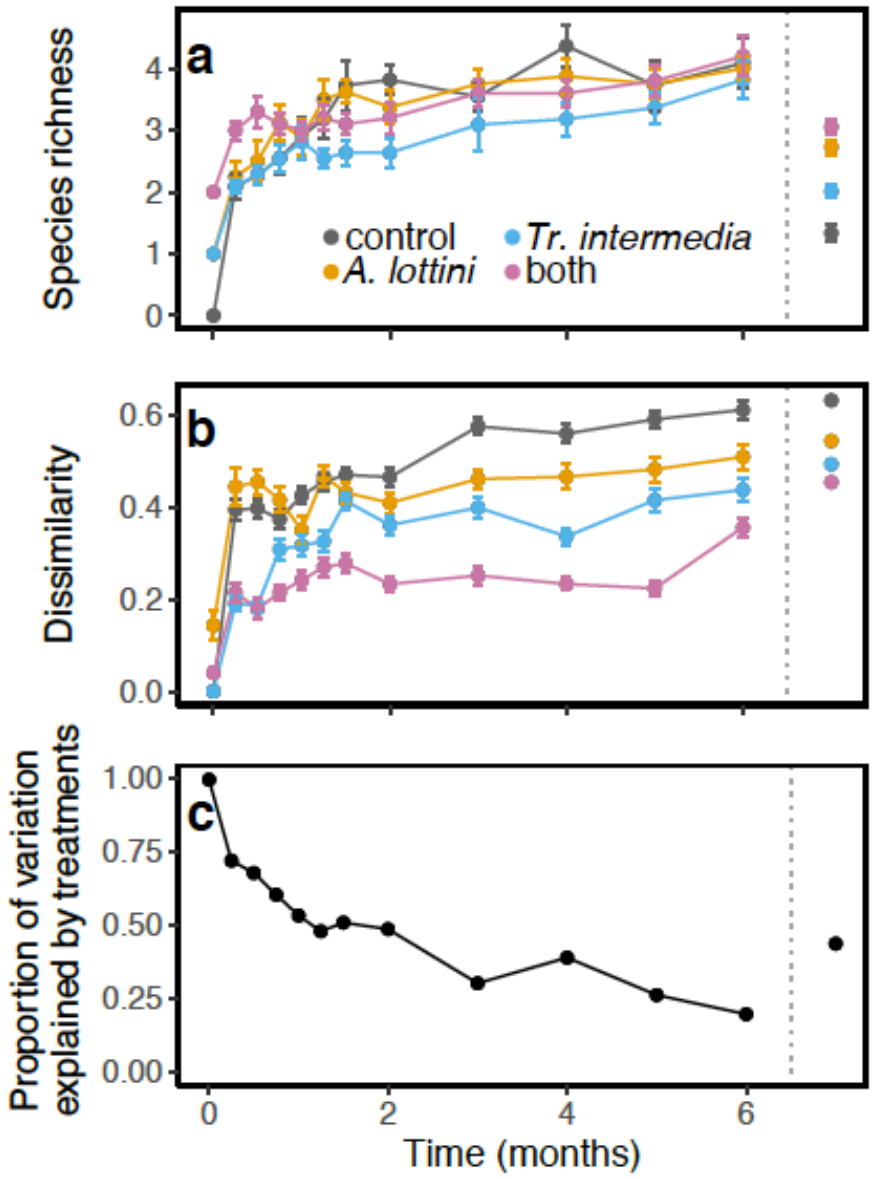

Figure 4.4. (a) Species richness at the coral level and (b) Jaccard dissimilarity at the coral pair level for the colonizing community through time, grouped by treatments. In both plots, points are mean values ± standard errors. Species abundance (Fig. 4.S3) follows a very similar pattern to species richness. (c) The proportion of variation in the composition of the colonizing decapod community explained by treatment group from PERMANOVA analyses run at each time window separately. In each panel, the data points to the right of the vertical dashed line are from surveys of naturally occurring communities around O‘ahu (n=321, surveyed once).

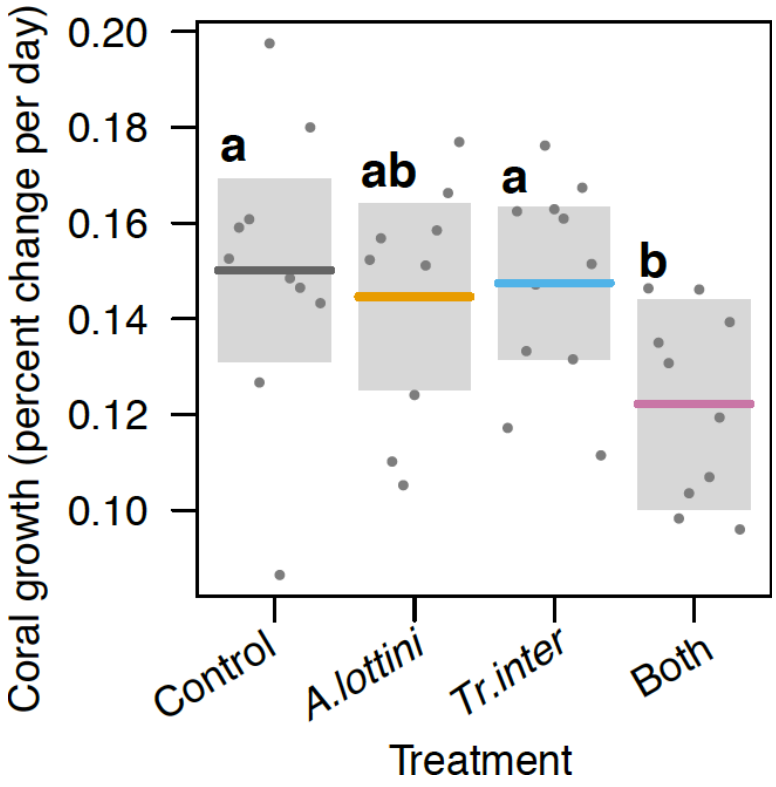

Figure 4.5. Model output for coral growth (percent change per day) from the colonization experiment (coral sizes measured as buoyant weights). Tukey HSD tests were used *post hoc* to identify significant differences between groups. Treatment was significant in the model ($p=0.029$); groups with the same letter are not significantly different.

Table 4.S1. Family, genus, species, classification as mutualist (mu), commensal (co), or facultative (fa) relative to *Pocillopora meandrina* (based on existing literature, e.g., Coles 1980, Black and Prince 1983, Stella et al. 2011, Britayev et al. 2017), and summaries of occurrence and frequency for all mobile decapod species observed across surveys of a colonization experiment, an establishment experiment, and naturally occurring communities around O'ahu (n=321).

Decapod identity			Colonization experiment		Establishment experiment		Natural
Family	Genus & species	mu co fa	Total number of colonizers	% of corals (n=40)*	% of corals (n=40)*	% of corals at month 6	% of corals (n=321)
Alpheidae	*Alpheus lottini*	mu	29	42.5	57.5	50.0	0.9
	Synalpheus charon	mu	41	62.5	7.5	5.0	0.3
Trapeziidae	*Trapezia bidentata*	mu	2	5.0	--	--	7.8
	Trapezia digitalis	mu	27	42.5	27.5	15.0	22.1
	Trapezia flavopunctata	mu	--	--	--	--	5.6
	Trapezia intermedia	mu	32	52.5	40.0	22.5	3.4
	Trapezia tigrina	mu	17	30.0	70.0	37.5	30.8
Xanthidae	*Etisus demani*	co	--	--	10.0	0.0	--
	Domecia hispida	co	20	35.0	40.0	10.0	2.2
	Pseudoliomera speciosa	co	1	2.5	--	--	3.4
Palaemonidae	*Harpiliopsis depressa*	co	530	100.0	100.0	97.5	37.7
Portunidae	*Thalamita coerulipes*	fa	341	92.5	57.5	25.0	0.3
	Charybdis hawaiensis	fa	--	--	--	--	0.9
Grapsidae	*Percnon planissimum*	fa	1	2.5	--	--	2.5
Majidae	*Schizophroida hilensis*	fa	--	--	2.5	0.0	--
Paguroidea	unidentified	fa	14	27.5	47.5	32.5	6.5
Stomatopoda	*Gonodactylaceus falcatus*	fa	10	25.0	32.5	12.5	0.3
Hippolytidae	*Saron marmoratus*	fa	--	--	--	--	0.6
	Saron neglectus	fa	--	--	--	--	0.6
Hymenoceridae	*Hymenocerca picta*	fa	--	--	--	--	0.3
Stenopodidae	*Stenopus hispidus*	fa	--	--	--	--	0.3

*Cumulative for all surveys.

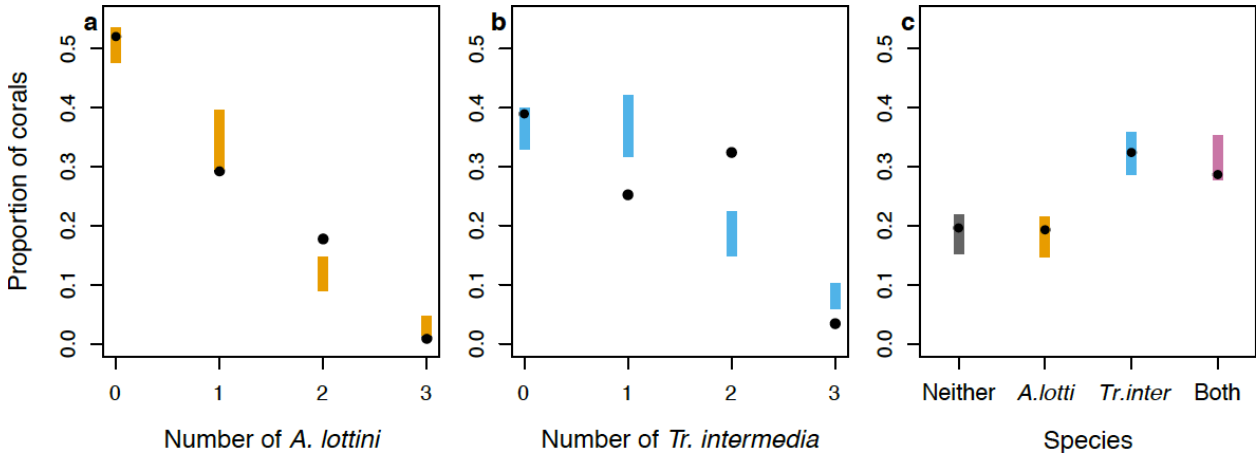

Figure 4.S1. The natural distribution of *A. lottini* and *Tr. intermedia* from surveys of 321 *Pocillopora meandrina* coral colonies around O'ahu (within the size range of experimental corals and with at least 50% live tissue, Counsell et al. 2018). (a) The proportion of corals with 0, 1, 2, or 3 *A. lottini*; (b) with 0, 1, 2, or 3 *Tr. intermedia*; and (c) with *A. lottini* only, *Tr. intermedia* only, neither species, or both species. Colored intervals represent the null distributions of occurrence if individual *A. lottini* and *Tr. intermedia* were distributed independently of other *A. lottini* and *Tr. intermedia* individuals (10,000 null distributions of the natural occurrence survey data were generated by randomly assigning each of the observed *Tr. intermedia* and *A. lottini* to one of 321 surveyed colonies generated with function "permatfull" in *R* package *vegan*; Oksanen et al. 2017). For both *A. lottini* (a) and *Tr. intermedia* (b), pairs were more common than expected, and singletons and triads were less common than expected with a random distribution of individuals. Joint occurrence of *A. lottini* and *Tr. intermedia* (c) fell within the null distribution, indicating that these two species were randomly distributed with respect to each other.

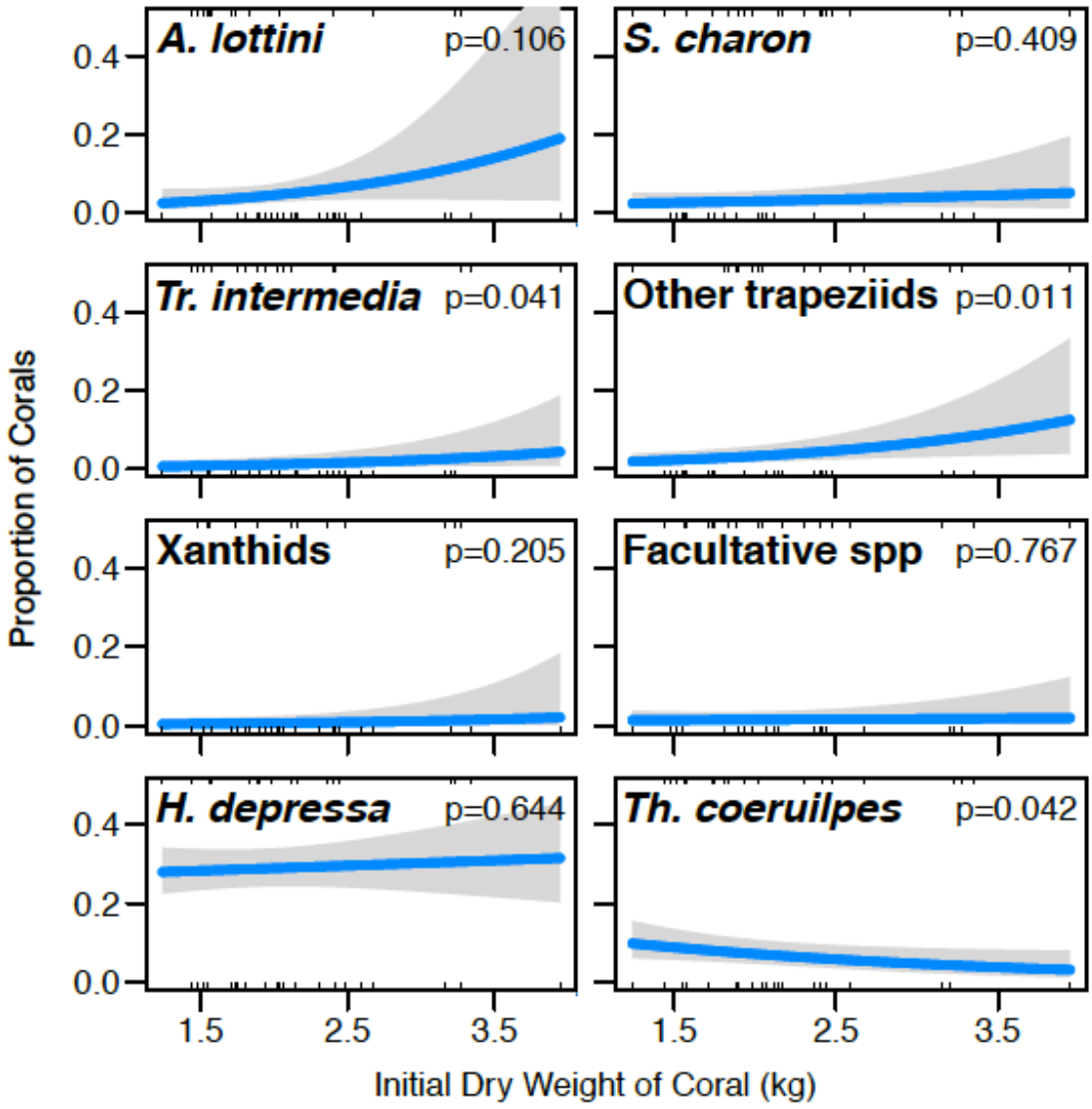

Figure 4.S2. Plots of the average proportion of corals across a gradient of coral colony sizes for which a colonizer type was observed from GLMMs. Each model included treatment (Fig. 4.2) and colony size as fixed effects (Table 4.1), and treatment block as a random effect. Gray bars show 95% confidence intervals on model estimates.

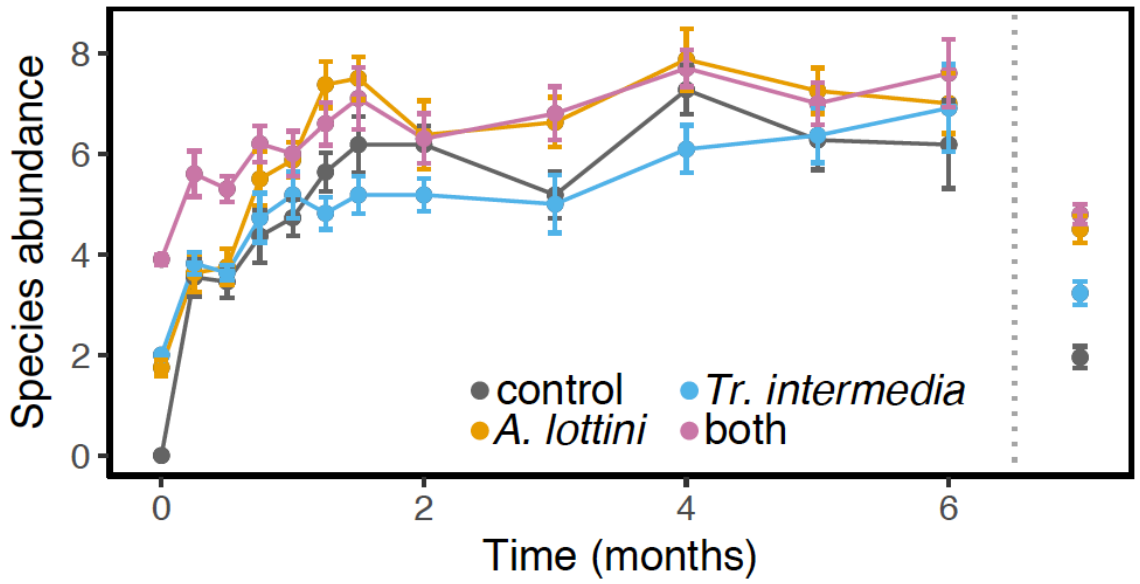

Figure 4.S3. Mean (± standard error) colony level species abundance during a community establishment experiment for four treatments. Patterns are very similar to those of species richness (Fig. 4.4a). The data points to the right of the vertical dashed line are from surveys of naturally occurring communities around O‘ahu (n=321, surveyed once).

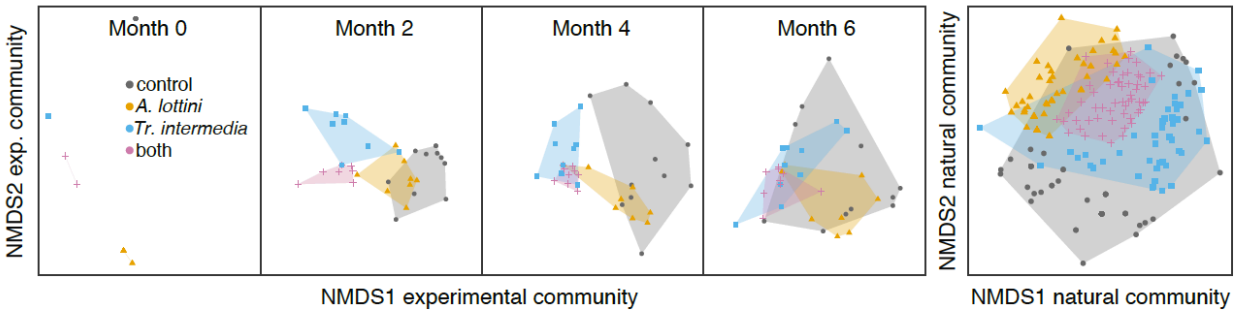

Figure 4.S4. NMDS plots (k=2; stress=0.1846) through time for the decapod community on corals manipulated at month 0 to have a pair of *A. lottini*, a pair of *Tr. intermedia*, a pair of both, or neither (control treatment). A NMDS plot (k=2; stress=0.2209) based on surveys of natural communities (n=321) separated based on natural presence of *A. lottini* and/or *Tr. intermedia*. In all plots, community composition is shown as axis scores from non-metric multidimensional scaling (function "metaMDS" in *R* package *vegan*; Oksanen et al. 2017).

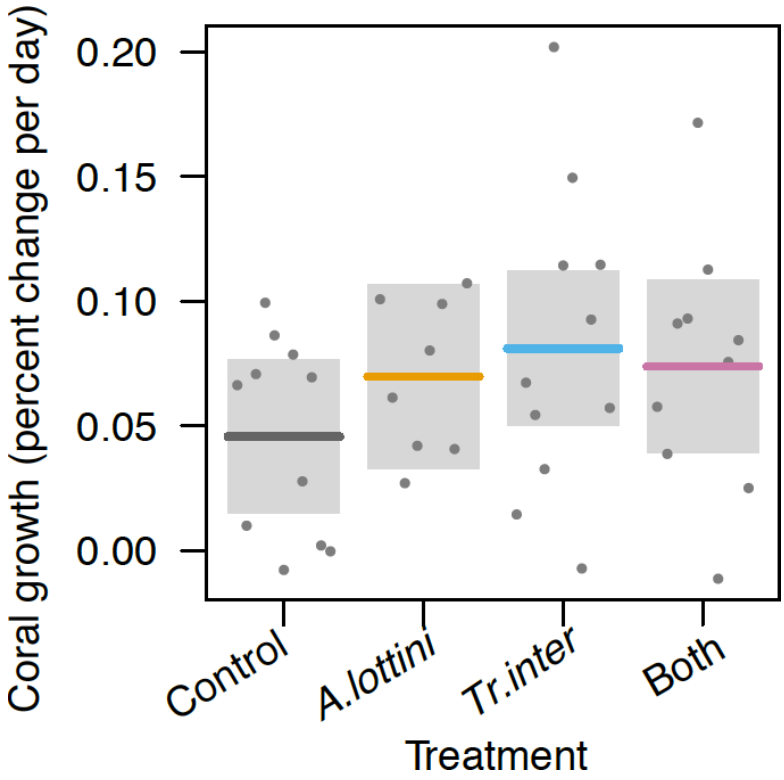

Figure 4.S5. Model output for coral growth (percent change per day) from an establishment experiment (coral sizes estimated from photographs taken at month 0 and month 6). At month 0, corals were manipulated to have a pair of *A. lottini*, a pair of *Tr. intermedia*, a pair of both, or neither (control treatment), and then communities were followed through time as other individuals colonized and became established on the corals. Treatment did not have a significant effect on coral growth (p=0.148).

CHAPTER 5

Conclusions

This dissertation investigated community assembly dynamics in a coral-associated cryptofaunal reef community. Observational studies were performed over spatial and temporal scales, and patterns in community composition were analyzed relative to colony- and site-scale environmental gradients. Potential support of species interactions as a structuring mechanism for communities was considered based on non-random spatial and temporal patterns in species occurrence. A community experiment was conducted to directly test for species interactions and to quantify priority effects of protection mutualists with the host coral on the formation and maintenance of the community associated with the host coral.

Main findings

In Chapter Two, patterns in coral-associated cryptofaunal communities were investigated over spatial scales. From surveys of 751 communities, greater variation in community abundance and species richness was found at the colony-scale than at the site-scale. Both of these community metrics increased with increasing colony size (i.e., habitat area) and wave height (i.e., disturbance), and decreased with increasing chlorophyll-a (i.e., productivity). In addition to re-emphasizing the importance of these three environmental drivers, species-specific patterns highlighted changes in community composition along gradients of depth and percent live coral tissue. The suite of potential drivers considered explained some colony-scale variation; however, a large amount of colony-scale variation remained unexplained, suggesting the importance of additional, unmeasured colony-scale factors. Of the 19 species that occurred on at least 5% of corals, the common guard crab *Trapezia intermedia* exhibited unique occurrence patterns in a variety of analyses, even in comparison to four other trapeziid species.

In Chapter Three, the consistency through time of communities associated with *P. meandrina* was documented. The communities associated with 42 colonies were surveyed from June 2014 to November 2017, for a total of 1,437 unique colony-in-time surveys. Within-colony community variation increased through time but did not exceed average between colony community variation. Thirty-four species were found to have stronger associations with individual host colonies than expected given a random distribution across colonies. In addition to

known mutualists and parasites for the host coral, this included 25 species with unknown effects on the growth and survival of the host coral. Temporal fluctuations in community composition and diversity metrics were not consistently correlated with concurrent fluctuations in regional environmental conditions. High colony-scale variation was observed in the model of within-colony community variation over a temporal gradient, and the importance of colony-scale parameters was reemphasized in the analyses of temporal shifts in community composition. Transition probability models illuminated species-specific positive and negative effects on arrival and departure dynamics among trapeziid crab species and among Scorpaenidae fishes.

In Chapter Four, the effects of two protection mutualist species on community formation and maintenance were directly investigated through a two-stage, field-based experiment. Both species exhibited inhibitory priority effects with evidence for species-specific competitive exclusion. Inhibitory effects were observed on the colonization of coral-mutualists, commensal species, and species that have a facultative association with the host coral. Species-specific trajectories through time varied across treatments with patterns that suggested order of arrival matters more for the outcome of species interactions between functionally similar species than between pairs of species from different functional groups, which appear to have more deterministic outcomes from their species interactions. This research also showed lower host coral growth in colonies with both mutualist species than in colonies with neither mutualist, suggesting context dependency of the benefits these mutualist species provide to their host coral, particularly in the absence of highly destructive corallivores (e.g., the crown-of-thorns sea star).

Future directions

Observed spatial patterns showed higher colony-scale than site-scale variation in coral-associated communities; however, these surveys were restricted to survey sites around the island of Oʻahu. To investigate the importance of regional environmental gradients over a larger spatial scale, I have surveyed a total of 1,956 communities from sites spanning across the Hawaiian archipelago (i.e., survey sites around the island of Hawaiʻi, Maui, Oʻahu, French Frigate Shoals, Lisianski, and Midway Atoll). In addition to investigating the effect of the environmental drivers considered in Chapter Two across larger spatial scales, I am interested in using this dataset to compare bottom-up and top-down drivers of variation in community composition. The

complexity of the habitat surrounding the host coral may have a bottom-up effect on species recruitment, migration, and survival rates within host coral-associated communities. The results of both spatial (Chapter Two) and temporal (Chapter Three) surveys emphasized colony-scale variation that was not fully accounted for by the coral quality metrics included in analyses. While it is likely that cryptofaunal communities are responding to colony characteristics unrecognized by the human observer, variation in the habitat immediately adjacent to the host coral could also be driving some of this unexplained colony-scale variation. The regional abundance of predators could exert a top-down control on species recruitment, migration, and survival rates within coral-associated cryptofaunal communities. As a postdoctoral researcher at the Hawai‘i Institute of Marine Biology (HIMB), I am investigating the role of these potential bottom-up and top-down drivers using photos of each surveyed coral to quantify the quality of the habitat surrounding each host coral and the National Oceanic and Atmospheric Administration's (NOAA) reef fish survey database to estimate site-scale predator abundance.

The importance of colony-scale parameters within the temporal surveys (Chapter Three) was somewhat surprising given the relatively similar characteristics of these colonies including comparable depths within each site and a restriction to colonies that were above 80% live coral tissue. Given the repeated emphasis of habitat quality at the colony scale, I would like to investigate how the community shifts in response to declining host coral health. For my temporal surveys, I followed 68 focal colonies ranging from 0 to 100% live. To study the consistency of these communities through time in Chapter Three, these data were subset to include only the healthy colonies. As a postdoctoral researcher, I will characterize shifts in the community composition synchronous to declines in the health of the host coral utilizing the subset of colonies that progressed through declines in live tissue. This work will include a comparison of community turnover rates between healthy colonies and colonies exhibiting a decline in live tissue. In addition, I will describe the progress of live tissue loss for these colonies and use a Cox proportional hazards analysis to model mortality rates for *P. meandrina*.

The results of all three data chapters suggested intriguing species interactions among trapeziid crabs. Further investigation into the potential colonization-competition dynamics between these species could include mesocosm experiments, surveys focused on recruit frequencies, and analyses of genetic connectivity. The priority effects experiment (Chapter Four)

suggested a context dependency of the benefits protection mutualists provide to their host coral in the absence of highly destructive corallivores. Mesocosm experiments could be used to quantify variation in these mutualisms associated with different combinations of mutualist species and for varying degrees of sedimentation. Mesocosms could also be used to quantify the effects of commensal species that exhibited strong site attachment relative to their host coral (Chapter Three) on coral growth. The community assembly experiment (Chapter Four) found priority effects of two mutualist species on the invertebrate community associated with *P. meandrina*. Alternatively, the presence of these established mutualist species had little to no effect on the recruitment of damselfish. As a postdoctoral researcher, I will investigate the spatial and temporal patterns in observed recruitment pulses of damselfish across the experimental array of corals established for Chapter Four. This work includes collaboration with HIMB geneticists to evaluate kinship patterns among setting cohorts of damselfish.

Research significance

This dissertation characterized the community associated with *P. meandrina* around Hawai‘i, described patterns in the composition of this community over spatial and temporal scales, correlated community variation with environmental gradients, and directly quantified the affect of two commonly occurring coral mutualist species on the formation and maintenance components of community assembly. The results illuminate patterns in the natural variation of this model reef community and provide an improved context for future research on this community. The results highlight intriguing patterns associated with specific environmental drivers and specific species suggesting focal components of this community for future research. In addition, the set of analyses utilized for Chapter Two and Chapter Three can serve as a template for community ecologists working to characterize patterns in the composition of communities over spatial and temporal gradients.

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